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## RESEARCH ARTICLE

# The relative influences of long-term fire management and woody cover on termite abundance and activity in an Australian tropical savanna

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## Abstract

1. Tropical savannas typically experience high fire frequencies, with prescribed fire commonly used as a management tool. Termites play an important role in the ecological functioning of tropical savannas, yet we have a limited understanding of how fire affects these important ecosystem engineers. To account for the effects of fire management on ecosystem structure and function, we need to understand the links between fire management and termite communities.
2. This study used a long-term (18-year) fire experiment in a tropical savanna near Darwin, northern Australia, to investigate the effects of different fire regimes on termite species composition, abundance and activity. We measured termite abundance and activity using a combination of baiting and reduced transect survey methods and compared these with fire activity (summarised fire frequency and intensity) and woody cover.
3. Termite species richness was similar across all fire treatments, and the level of fire activity had a minimal effect on species composition, which was more strongly influenced by woody cover. Wood-feeding termite abundance and the consumption of wood baits were negatively correlated with fire activity and positively correlated with woody cover. Soil/wood interface-feeding termites showed no correlation with fire activity but a positive correlation with woody cover. Significant negative mediation effects of fire activity through woody cover were detected on the abundance of wood- and soil/wood interface feeders and wood and straw bait consumption. Grass-feeding termites were encountered too infrequently to draw conclusions about their correlation with fire activity and woody cover; however, straw bait consumption was positively correlated with fire activity.
4. *Synthesis and applications.* The effects of fire on termite abundance and activity are primarily indirect, mediated through changes in vegetation structure. As high fire activity is associated with reduced woody cover, maintaining regimes of frequent, high-intensity fires over the long term has the potential to affect

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ecosystem function. While minimising the occurrence of high-intensity, late dry season fires is consistent with fire management goals in these savannas, care is still required to avoid the negative consequences of high fire frequencies.

#### KEYWORDS

ecosystem function, fire, management, species composition, species richness, termites, tropical savanna

## 1 | INTRODUCTION

Fire is a frequent disturbance and land management tool in savannas around the world (Kelly et al., 2023). Tropical savannas are fire-dependent ecosystems and the dominance of grasses relies on burning; without fire, these ecosystems can be replaced by forests (Bond et al., 2005). In addition to natural fire patterns, regular prescribed, low-intensity fires are commonly used to reduce the likelihood of severe late dry season fires. These prescribed fires are often performed with the aim of earning carbon credits through greenhouse gas abatement programs (Russell-Smith et al., 2013). These programs use prescribed early dry season fire to reduce the extent and severity of fires and thus greenhouse gas emissions (Russell-Smith et al., 2013). In Australia, greenhouse gas abatement programs now cover 25% of the northern savannas (Edwards et al., 2021), and most areas are burned every 1–4 years (Corey et al., 2019). With such widespread regular application of prescribed fire, it is critically important to understand how different fire regimes affect ecosystem structure and function.

Termites are important ecosystem engineers and fulfil many key ecological functions, including as decomposers, nutrient cyclers, manipulators of soil structure and creators of habitat for wildlife (Griffiths et al., 2019; Jouquet et al., 2011; Mando et al., 1996; Woolley et al., 2018). Despite their importance in many ecosystems, little is known about the effects of fire regime on termites in tropical savannas, especially when maintained over the long term.

Of the few studies investigating the effects of fire on termites, the results have been mixed and vary according to the fire regime attributes and termite feeding groups examined. Studies from Australia have either examined single fire events or relatively short-term experimental fire treatments. In some cases, termite abundance has been shown to decrease following fire (Abensperg-Traun & Milewski, 1995; Dawes-Gromadzki, 2007)—particularly of those species that feed on live wood (Braithwaite et al., 1988). In other cases, termites that feed on dead wood, soil or grasses were seen to increase with fire (Braithwaite et al., 1988). Studies from Brazil (Desouza et al., 2003) and South Africa (Davies et al., 2012) found little or no effect of fire, suggesting that the subterranean habits of termites provided protection from the direct effects of fire. While the direct effects of fire on termites may be minimal, the long-term effects of repeated fire over several years may have stronger indirect effects on termites. In a long-term South African experiment, repeated fires were found to cause changes in vegetation structure and thus in the food and shelter resources available to termites (Davies et al., 2012).

The concept of the effects of fire being indirect through changes in vegetation structure has been further developed by Andersen (2019) and Andersen (2021), and recently confirmed for ants by Brassard et al. (2023). In an Australian tropical savanna, fire regime explained little variation in ant communities, but ant species frequency and richness were negatively related to woody vegetation cover (Brassard et al., 2023). This lack of response to fire but sensitivity to vegetation changes supports the hypothesis that the effects of fire are primarily indirect, through changes in vegetation. No studies have investigated the long-term effects of fire on termites in Australian tropical savannas.

A long-term (18-year) fire experiment in a mesic tropical savanna in northern Australia offered an ideal opportunity to investigate the long-term effects of fire on termites in these ecosystems. The fire experiment includes six different fire regime treatments, ranging in frequency from annual to unburned, and in seasonality from early dry season to late dry season fire. These fire treatments have been previously shown to produce large changes in vegetation structure, with tree biomass and woody cover decreasing markedly with increasing fire frequency and severity (Levick et al., 2019). As vegetation structures such as woody cover represent food and shelter resources for termites, fire and any resulting changes to vegetation cover are likely to have consequences for termite abundance and activity. By surveying termite communities after 18 years of experimental fire treatments, we hypothesise that the effects of fire on termite abundance and activity will primarily be indirect and negative, through reductions in vegetation cover. By testing this hypothesis, we aim to inform sustainable fire management that supports the ongoing contribution of termites to ecosystem function in tropical savannas.

## 2 | MATERIALS AND METHODS

### 2.1 | Study area and design

The study area was located at a long-term (18-year) fire experiment at the Territory Wildlife Park in Berry Springs in the Northern Territory, Australia (12°70' S, 131°00' E; Figure S1). The climate is wet-dry tropical, with average annual daily minimum and maximum temperatures of 22.0 and 34.4°C, and a mean annual rainfall of ~1700 mm (BOM, 2024). The rainfall is highly seasonal and predominantly falls in the wet season from November to April

(Richards et al., 2012). The vegetation is savanna, with a canopy dominated by *Corymbia bleeseri*, *Eucalyptus miniata* and *Eucalyptus tetrodonta*, and a grassy understorey dominated by species of *Pseudopogonatherum*, *Sarga* and *Eriachne* (Richards et al., 2012; Scott, 2008). The soils are lateritic red earth consisting of brown sandy or clay loams, with variable levels of gravel across the experiment (Scott, 2008).

The long-term fire experiment features 18 × 1 ha plots oriented north to south. The 18 plots comprise three replicates of six different fire treatments: early dry season burns (the first week of June) every year (E1), and every two (E2), three (E3) and five (E5) years, as well as late dry season burns (the first week of October) every 2 years (L2) and unburned treatments (U; Figure S1). The fire experiment was established in 2004 (Parr et al., 2007) and so, at the time of sampling, fire treatments had been maintained for 18 years. The Territory Wildlife Park gave permission for fieldwork to occur on their grounds.

## 2.2 | Termite sampling

We sampled termites using baiting and reduced transects in each of the plots. Sampling was conducted between February and May 2022, during the wet and transition seasons to maximise sampling success (Dawes-Gromadzki & Spain, 2003). For full details of the baiting and reduced transect (active searching) methods, see Rochelmeyer, Richards, et al. (2024). In brief, baiting used a 3 × 9 baiting grid consisting of three wood baits and three paper baits (standard in baiting protocols), as well as three straw baits (added to sample grass-feeding termites, e.g. Evans et al., 2011), alternating positions in each row and spaced 5 m apart (Figure S1). Wood and paper baits were buried, and straw baits were pegged to the surface. We checked and returned the baits to the same position after 4, 7 and 10 weeks had passed following placement. Following Dawes-Gromadzki (2003), we estimated the percentage of bait consumed when each bait was checked. We used a reduced transect method designed for savannas (Davies et al., 2021) to actively search for termites in each plot. We used two replicated reduced transects of 60 × 2 m for each plot, with each transect divided into 5 × 2 m quadrats, each of which was searched for 10 min. Transects were positioned between the baiting rows, 5 m from each row (Figure S1). Active searches were conducted during daylight hours and involved searching for termites in the soil, leaf litter, termite mounds, dead wood and galleries on trees. Soil was searched with a trowel a minimum of six times in each quadrat, to the depth of the trowel (~15 cm). Termites were collected under Permit 70490 under the Territory Parks and Wildlife Conservation Act 1976.

## 2.3 | Termite identification and grouping

When termites were encountered at baits, transects or mounds, at least three soldiers were collected where possible and stored in

100% ethanol for identification. Termites were identified to species using Hill (1942) and Miller (1991). Voucher specimens were lodged with the Museum and Art Gallery of the Northern Territory, Darwin. We defined an 'encounter' following Davies et al. (2021), where an encounter was recorded each time a species was found at a bait or section of transect. Bait encounters were pooled with transect encounters for total species encounter numbers.

As we hypothesised that termite responses to fire would be due to related changes in vegetation structure, we grouped termites according to three broad food substrate categories: grass feeders, wood feeders and soil/wood interface feeders (defined as termites that feed either at the interface of decomposing vegetation and soil or on soil itself). These food substrate categories represent the broad food resources that termites consume and which are likely to have different responses to fire.

## 2.4 | Environmental variables

### 2.4.1 | Fire

Although the plots are part of a long-term fire experiment, the low replication of three plots in each of the six different fire treatments has resulted in high within-treatment variation (Figure S2) and limited statistical power. Therefore, we did not use the treatments as factors but used a previously published index of fire activity for each plot that summarised both the frequency and intensity of fires over the 18-year history of the experiment (Brassard et al., 2023, 2024). While fire activity is not a metric directly used by fire managers, this index allowed us to maximise the explanatory power of our limited dataset and investigate relationships between fire and termites—the knowledge of which can then be used by land managers. Fire activity was calculated as the sum of fire intensity values for a plot since the first year of the experiment in 2004 (Figure S2). Byram fire-line intensity values ( $\text{kW m}^{-1}$ ) represent the energy released along the fire front (Byram, 1959) and are calculated as the product of fuel heat yield, fuel load and the rate of spread of the fire (Williams et al., 1998). Fuel heat yield was estimated at  $20,000 \text{ kJ kg}^{-1}$  for northern Australian savannas (Williams et al., 1998). Fuel load was calculated before each experimental fire by harvesting and weighing ten  $0.5 \times 0.5 \text{ m}$  fuel samples per plot (Levick et al., 2019). Rate of spread was determined using either thermocouples (six per plot) or manual timing by observers with stopwatches (Levick et al., 2019).

The full record of fire intensity values is incomplete for this experiment, with some fires being too dangerous to measure the rate of spread in situ. In such instances, we estimated fire intensity using post-fire assessments of vegetation scorch height following Brassard et al. (2024). Scorch height is strongly related to fire intensity (Williams et al., 1998), and missing intensity values were estimated using the relationship between previously recorded fire intensity values and vegetation scorch heights from this experiment. Refer to Brassard et al. (2024) for more detail regarding estimating fire intensity values at this experiment.

## 2.4.2 | Woody vegetation cover

We estimated woody vegetation cover (before fire) using terrestrial laser scanning (TLS) between May and July 2022. We scanned each plot using a Riegl VZ-2000i LiDAR system mounted on a vehicle (10 perimeter scans) and on a tripod (two internal scans). The scanner was operated at 600kHz, with an angular sampling resolution of 30 mdeg. We processed the TLS data following Levick et al. (2021), using Riegl's RiSCAN Pro software suite (v2.17) to co-register the scans and the LAStools suite (rapidlasso GMBH, 2024) for ground classification, height normalisation and canopy height model (CHM) production. The fraction of vegetation cover was estimated from CHMs with a spatial resolution of 0.1m. We used a height threshold of 2m to capture the cover of woody vegetation (dead or alive) above this height, thus excluding the tall annual grass layer that is present in many plots and coarse woody debris.

## 2.4.3 | Grass cover

Grass cover was quantified in each plot in 2019 (S. Bryceson, unpublished data). Fire frequency was strongly correlated with the cover of annual grass species (primarily Andropogoneae; Bryceson et al., 2023; S. Bryceson, unpublished data). Consequently, we used the cover of these grass species for our grass cover variable, which was quantified as the percentage cover of annual grass species in 10×10m contiguous quadrats throughout each plot, excluding a 20m buffer from all edges. The grass cover value of each quadrat was then used to calculate mean grass cover for each plot.

## 2.5 | Data analysis

In order to investigate community-level termite responses to fire, we assessed species composition by fire activity and woody cover using distLM (distance-based linear models) multivariate analysis in PRIMER v7 (Clarke & Gorley, 2015; Legendre & Anderson, 1999). We square-root-transformed the number of encounters for each species in a plot to more equally weight common and rare species (Clarke & Warwick, 2001), then created a resemblance matrix using Bray–Curtis similarity. The environmental variables were normalised, and then a resemblance matrix was created using Euclidean distance. Marginal and sequential tests (with selection using the step-wise procedure and AICc [Akaike's information criterion]) were used to determine the variance in species composition explained by each environmental variable separately and cumulatively. We then used a distance-based redundancy analysis (dbRDA) ordination to visualise the differences in species composition between plots.

Analyses of termite relative abundance (where the number of encounters was used as a surrogate for abundance; Davies et al., 2012, 2021) and level of activity (proportion of bait consumed) in response to fire were undertaken using generalised linear mixed effects models (GLMM) in the package 'glmmTMB' (Brooks et al., 2017) in the

software R (v4.2.2; R Core Team, 2024). Prior to running the models, we checked the data for dependency, outliers and collinearity between covariates. Fire activity was strongly correlated with woody cover and grass cover (Pearson correlation coefficients of  $-0.75$  and  $0.81$ , respectively), while woody cover and grass cover were also highly negatively correlated (Pearson correlation coefficient =  $-0.82$ ; Figure S3). Consequently, models were run separately for each covariate. Due to the strong collinearity between fire activity and grass cover, and the similar responses of termites to these variables, we have presented only the results of fire activity models to assist with interpreting the implications for fire management.

As changes in termite abundance in response to fire may vary according to food substrate (grass, wood or soil/wood interface), analyses with termite abundance as the response included the interaction with food substrate. Similarly, because changes in bait consumption might vary with the termite species feeding on the baits and consequently the type of bait, analyses for termite activity included the interaction with bait type. All analyses included plot as a random effect to account for the nesting of food substrate or bait type within each plot.

The GLMM analyses of the number of termite encounters used the Poisson distribution, and analyses of the proportion of bait consumed used the beta distribution. We validated the models using the 'DHARMA' R package (Hartig, 2022), including testing for overdispersion and homogeneity of variance of the residuals. For the final models, we obtained estimates and *p* values for each level of substrate and bait type against fire activity or woody cover by reordering the factor levels.

We used mediation models to test the direct and indirect effects of fire on termite abundance and activity. Mediation occurs when the effect of the independent variable on the dependent variable is indirect and transmitted through a third variable—the mediator (Agler & De Boeck, 2017). Here, we tested the effects of fire (the independent variable) and fire through vegetation cover (the mediator) on the abundance of each termite food substrate and the consumption of each bait type (the dependent variables). All models were tested with woody vegetation cover as the mediator, except straw bait consumption, which was also tested with grass cover as the mediator. We generated initial models using standardised variables and following the steps of Baron and Kenny (1986), then checked model assumptions using the 'gvlma' (Pena & Slate, 2019) and 'performance' (Lüdtke et al., 2021) R packages. Due to the low number of encounters with grass-feeding termites, we were unable to test mediation effects for this group. To test the statistical significance of mediation, we used bootstrapping (1000 simulations) with the 'mediation' R package (Tingley et al., 2014) to quantify the direct (fire only), indirect (fire through vegetation cover) and total effects (sum of direct and indirect effects) on the dependent variables.

## 3 | RESULTS

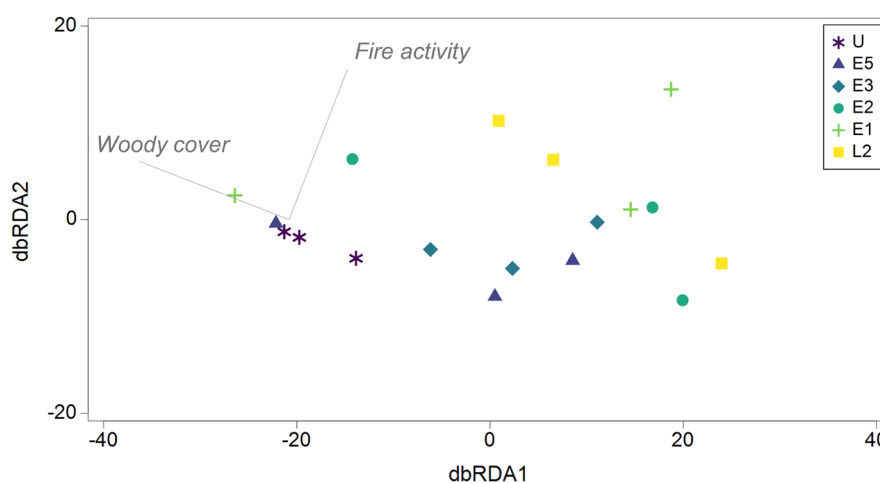
A total of 1105 termite samples were collected across the baiting, transect and mound surveys, with 32 species identified (Table S1).

Species richness was similar across all treatments, with 22–23 species identified in each treatment (Table S1). Wood-feeding termites had the highest species richness and number of encounters across the entire experiment (16 species, 831 encounters), followed by soil/wood interface feeders (11 species, 253 encounters) and grass feeders (5 species, 21 encounters; Table S1).

distLM analysis found that fire activity and woody cover had significant effects on termite species composition. When considered separately, woody cover explained 24.1% of the variation in termite species composition ( $p=0.001$ ), and fire activity explained 13.8% ( $p=0.028$ ). When considered together, fire activity and woody cover explained 27.3% of the variation in termite species composition. The two axes of the dbRDA ordination were most strongly correlated with the cover of woody vegetation (dbRDA1) and fire activity (dbRDA2), explaining 24.1% and 3.2% of the total variation in

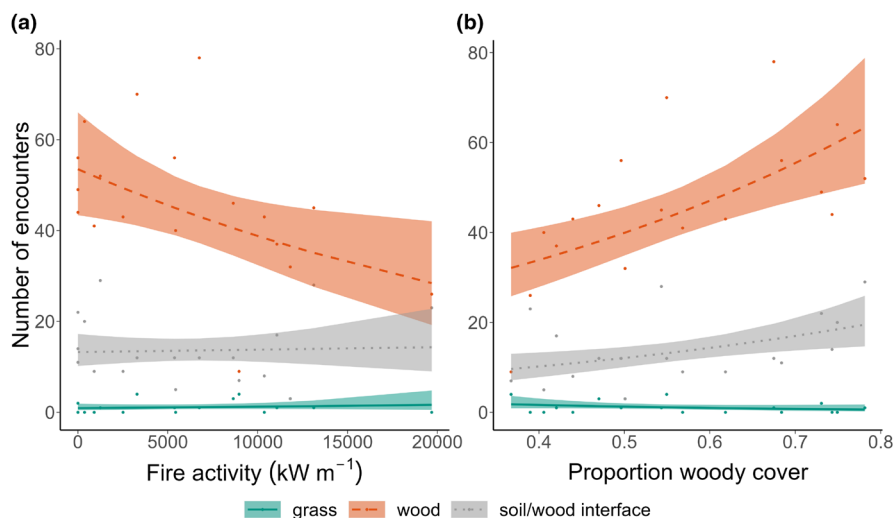
termite species composition, respectively (Figure 1). The three plots in the unburned treatment were relatively tightly clustered in terms of species composition compared to the plots in the five burned treatments (Figure 1; Figure S4).

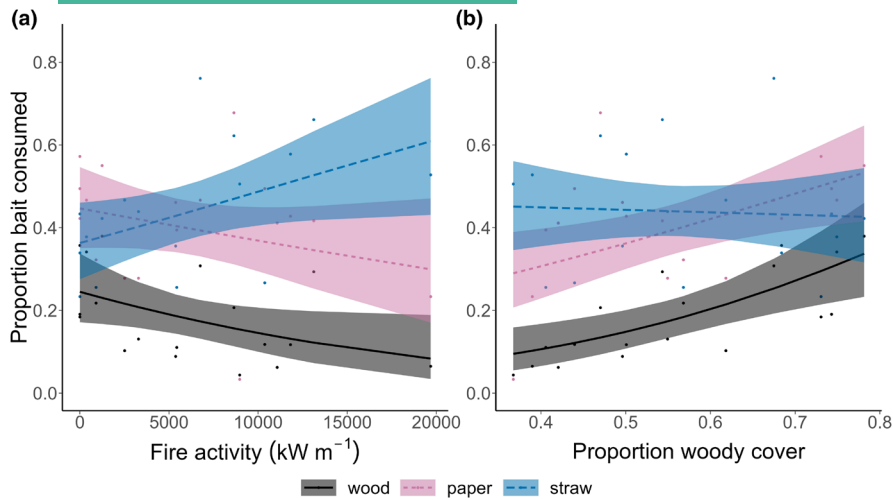
Wood-feeding termite abundance (number of encounters) was negatively correlated with fire activity (standardised estimate =  $-0.18$ ,  $p=0.017$ ) and positively correlated with the proportion of woody vegetation cover (standardised estimate =  $0.22$ ,  $p<0.001$ ; Figure 2; Table S2). Soil/wood interface-feeder abundance showed no significant correlation with increasing fire activity (standardised estimate =  $0.02$ ,  $p=0.807$ ) and a positive correlation with increasing woody cover (standardised estimate =  $0.23$ ,  $p=0.005$ ; Figure 2; Table S2). Grass cover was highly correlated with fire activity and influenced termite abundance similarly, with wood-feeding termite abundance declining with increasing grass cover but no significant



**FIGURE 1** Ordination plot showing relationships between termite species composition and environmental variables. Ordination was generated using distance-based redundancy analysis (dbRDA) of the distance-based linear model (distLM) describing the relationship between environmental variables (fire activity and woody cover) and differences in termite species composition between plots. Vectors indicate the relative effect size of each environmental variable (length of vector) and correlation with the axes (direction of vector). The first axis (dbRDA1) correlates most strongly with woody cover (explains 24.1% of the total variation in termite species composition), while the second axis (dbRDA2) correlates most strongly with fire activity (explains 3.2% of the total variation). E1, burned early in the dry season every year; E2, burned early in the dry season every 2 years; E3, burned early in the dry season every 3 years; E5, burned early in the dry season every 5 years; L2, burned late in the dry season every 2 years; U, unburned.

**FIGURE 2** Relationships between the number of termite encounters and environmental variables. (a) The relationship between the number of encounters and fire activity ( $\text{kW m}^{-1}$ ). (b) The relationship between the number of encounters and the proportion of woody vegetation cover. The lines represent the predictions of generalised linear mixed models with 95% confidence intervals, and the points represent the original data. The three termite food substrates (grass-, wood- or soil/wood interface feeders) are shown separately.





**FIGURE 3** Relationships between the proportion of bait consumed and key predictors. (a) The relationship between the proportion of bait consumed and fire activity ( $\text{kW m}^{-1}$ ). (b) The relationship between proportion of bait consumed and the proportion of woody vegetation cover. The lines represent the predictions of generalised linear mixed models with 95% confidence intervals, and the points represent the original data. The three bait types (wood, paper or straw) are shown separately.

correlation with soil/wood interface feeders (Table S2; Figure S5). Due to the low number of encounters with grass-feeding termites, we were unable to detect differences between the abundance of these species and either fire activity or vegetation cover.

Wood bait consumption was negatively correlated with fire activity (standardised estimate =  $-0.36$ ,  $p = 0.040$ ) and the consumption of both wood (standardised estimate =  $0.51$ ,  $p < 0.001$ ) and paper (standardised estimate =  $0.33$ ,  $p = 0.009$ ) baits were positively correlated with woody vegetation cover (Figure 3; Table S2). There was no significant effect of fire activity on paper bait consumption (standardised estimate =  $-0.18$ ,  $p = 0.203$ ). Straw bait consumption increased with fire activity (standardised estimate =  $0.28$ ,  $p = 0.042$ ) and showed no strong correlation with woody vegetation cover (standardised estimate =  $-0.03$ ,  $p = 0.799$ ; Figure 3; Table S2). Grass cover was negatively correlated with wood bait consumption, had a significant negative effect on paper consumption and no detectable effect on straw consumption (Table S2; Figure S5).

We found significant negative mediation (indirect) effects of fire activity through woody cover on wood- (coefficient estimate =  $-21.38$ ,  $p = 0.034$ ) and soil/wood interface-feeding (coefficient estimate =  $-11.44$ ,  $p = 0.002$ ) termite abundances and on wood (coefficient estimate =  $-0.15$ ,  $p < 0.001$ ) and straw (coefficient estimate =  $-0.22$ ,  $p = 0.012$ ) bait consumption (Table S3). No significant direct effects of fire activity (without the influence of woody cover) could be detected on termite abundances or on wood and paper bait consumption (Table S3). Straw bait consumption retained a significant positive direct effect of fire activity (coefficient estimate =  $0.46$ ,  $p = 0.006$ ). We found no significant mediation effect of grass cover on straw bait consumption, but did detect a significant positive direct effect of fire.

## 4 | DISCUSSION

Our work supports the recent conceptual model of Andersen (2021) that posits that the effects of fire on fauna are primarily indirect, mediated through fire-driven changes in vegetation structure. Andersen's model has recently been shown to hold true for savanna

ants (Brassard et al., 2023). In line with Andersen's model, our results support the theory that fire-driven shifts in vegetation structure typically have a stronger effect on termite communities than the direct effects of fire.

We detected minimal influence of fire treatment on termite species richness or fire activity on species composition, and the cover of woody vegetation was the strongest variable affecting termite species composition. This is consistent with previous work from South African savannas, which has found that the abundances of certain termite species vary with canopy cover (Davies et al., 2012). Fire activity—which summarises both the frequency and intensity of fires over the life of the experiment—influenced the abundance and activity of termites differently depending on the termite food substrate and the bait type used to assess termite activity. For wood-feeding termites, abundance and activity were negatively associated with fire activity. This reduced abundance of wood-feeding termites in areas with higher fire activity contrasts with a previous long-term fire study in South Africa. Davies et al. (2012) observed that wood- and fungus-feeding termites were more abundant on annually burned plots, although this was also associated with sites of higher rainfall. In our study, the decline in wood-feeding termites with fire is likely due to related changes in habitat resources: plots with greater fire activity were associated with reduced cover of woody vegetation and thus food resources for those termite species. This reduction in woody cover with increased fire activity is consistent with other research in the region, where frequent high-severity fires have been shown to negatively affect tree recruitment, survival and growth (Murphy et al., 2023). Soil/wood interface-feeding termites did not respond to fire activity but increased with woody cover. The lack of response to fire by these species is likely due to their protective subterranean habits (Avitabile et al., 2015; Davies et al., 2012; Desouza et al., 2003), while their sensitivity to woody cover is likely due to their susceptibility to desiccation and temperature in more open and exposed habitats (Davies et al., 2012). The significant woody vegetation mediation effects with non-significant direct effects of fire indicate that the influence of fire in these cases is primarily through changes in vegetation structure.

Once any mediation effects had been accounted for, only straw bait consumption showed a significant positive direct effect of

fire, indicating that fire directly increases grass-harvesting activity. Unfortunately, due to the low number of encounters with grass-feeding termites, we were unable to confidently assess the relationship with the abundance of grass-feeding termites. While we were unable to identify responses of grass-feeding termites to fire or woody cover, we could still interpret differences in straw bait consumption. Our straw baits were analogous to dead, standing grass vegetation at our site, and so consumption of the straw baits gave an indication of grass-harvesting activity. The increase in straw bait consumption with fire activity may be associated with greater grass cover in more frequently and intensely burned plots. With increased availability of grass as a food resource, it is likely that the abundance and activity of grass feeders would also increase. Interestingly, when we tested for mediation effects of vegetation cover on straw bait consumption, there was no significant mediation effect of grass cover. Providing that a minimum quantity of grass is present at the site, it may be that the exact cover of grass is not an influential factor for the extent of grass-harvesting activity. Other conditions that affect termite abundance or activity, such as woody cover, may have a stronger influence on grass harvesting. Woody cover showed a significant negative mediation effect on straw consumption, and if this is not due to a related reduction in grass cover as a resource, then it may be more related to conditions supporting termite occurrence and abundance, such as soil type, depth or moisture, which have been shown to vary across the plots (Scott, 2008).

The low number of encounters with grass-feeding species may be due to the species foraging at night. For example, some species of grass-feeding *Trinervitermes* in West Africa forage at night (Sands, 2011) and consequently are unlikely to be found in transects except in mounds. To avoid uncertainty as to whether low grass-feeder abundance is due to actual differences in abundance or ineffective sampling, future studies should consider including mound surveys for grass-feeding species. In addition, given the importance of woody cover for termites, future research could investigate the heterogeneity of woody cover in the landscape and the relative importance of using fire to manage this resource to support termite populations in the region. Our study focused on the responses of termites to fire in a relatively high rainfall (~1700 mm) tropical savanna. As termite responses to fire have been shown to vary with rainfall in South African savannas (Davies et al., 2012), future studies could investigate the consistency of termite responses along a rainfall gradient in Australian savannas. Additionally, fire is likely to affect other food resources for termites (such as coarse woody debris or woody litter) and consequently influence termite abundance and activity. Future studies investigating the effects of fire on other food resources and termites would be useful for a more comprehensive understanding of how fire can affect termites through changes in vegetation structure.

#### 4.1 | Synthesis and applications

Northern Australia experiences extremely high-fire frequencies, and in the absence of management, typical fire intensities are relatively high. With the disruption of traditional Aboriginal fire management

practices, contemporary fire regimes came to be characterised by frequent, high-intensity late dry season wildfires (Russell-Smith et al., 2013). By the end of the 20th Century, there were documented negative biodiversity impacts from these altered fire regimes on plant communities, mammals and birds (Russell-Smith et al., 2003). Through reducing woody cover, these frequent, high-intensity fire regimes have also likely had negative indirect effects on termite populations and their ecological functions (such as nutrient cycling and habitat creation). There is evidence that prescribed burning and the resulting reduction in typical fire intensities can lead to increases in live tree biomass and litter biomass (e.g. Murphy et al., 2023). Consequently, improved fire management since the turn of the century—which promotes low-intensity early dry season fires to reduce the frequency of high-intensity late dry season fires—is likely to be helping to restore woody cover, and subsequently, crucial ecological functions performed by termite communities.

The significant negative mediation effects of fire through woody cover and limited direct effects suggest that: (1) the effects of fire on termites are primarily indirect through changes in vegetation structure; and (2) that frequent, high-intensity fires over the long term (which are associated with reduced woody cover) have the potential to affect ecosystem function by changing termite communities. While reducing the risk of high-intensity, late dry season fires is consistent with the goals of fire management in Australian tropical savannas (Andersen et al., 2005), care is still required to avoid negative consequences of high fire frequencies. In addition, as woody cover was found to be the primary driver of termite abundance rather than fire, other disturbance mechanisms that alter vegetation structure (e.g. drought, tropical cyclones) may also have implications for termites and the ecosystem functions they perform.

#### AUTHOR CONTRIBUTIONS

Ellen Rochelmeyer conceived the ideas and designed the methodology with support from Anna E. Richards, Shaun R. Levick, Brett P. Murphy, Alyson M. Stobo-Wilson and Theo Evans; Ellen Rochelmeyer collected the data; Ellen Rochelmeyer analysed the data with support from Anna E. Richards, Shaun R. Levick, Brett P. Murphy, Alyson M. Stobo-Wilson, Paul Eggleton and Theo Evans; Ellen Rochelmeyer led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

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### CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest.

### DATA AVAILABILITY STATEMENT

Data are available via the CSIRO Data Access Portal <https://data.csiro.au/collection/csiro:62661> (Rochelmeyer, Evans, et al., 2024).

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## SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

**Figure S1.** Map of study site location and experiment design.

**Figure S2.** Fire intensity and fire activity values by fire regime treatment.

**Figure S3.** Relationships between fire activity, woody cover and grass cover.

**Figure S4.** Ordination plot showing relationships between termite species composition and environmental variables.

**Figure S5.** Termite responses to changes in grass cover.

**Table S1.** Comparison of number of encounters for each termite species.

**Table S2.** Summary of generalised linear mixed model outputs for termite abundance and bait consumption.

**Table S3.** Mediation analysis output.

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