Interactions among threats affect conservation management outcomes: Livestock grazing removes the benefits of fire management for small mammals in Australian tropical savannas

Sarah Legge1,2,3,4 | James G. Smith1 | Alex James1 | Katherine D. Tuft1,5 | Terry Webb1 | John C. Z. Woinarski4

1Australian Wildlife Conservancy, Mornington Sanctuary, Derby, Western Australia, Australia
2Fenner School of Environment & Society, The Australian National University, Canberra, Australian Capital Territory, Australia
3Centre for Biodiversity and Conservation Science, University of Queensland, St Lucia, Queensland, Australia
4Research Institute of Environment and Livelihoods, Charles Darwin University, Casuarina, Northwest Territories, Australia
5Arid Recovery, Roxby Downs, South Australia, Australia

Correspondence
Sarah Legge, 780 Koonyum Range Road, Koonyum Range, NSW 2482, Australia.
Email: sarah.legge@anu.edu.au, sarahmarialegge@gmail.com

Funding information
Australian Wildlife Conservancy; Australian Government: Caring For Our Country, National Environmental Research Program, National Environmental Science Program Threatened Species Recovery Hub; Western Australian Government Kimberley Science and Conservation Strategy; The Nature Conservancy’s David Thomas Challenge

Abstract
Conservation scientists and practitioners usually focus on understanding and managing individual threats to biodiversity. However, threats may interact, making management outcomes unpredictable. Here, we investigated whether interactions between fire regimes and introduced livestock affect the conservation goal of population recovery for small mammals in Australia’s tropical savannas, using a long-term and landscape-scale study. Mammal richness and abundance increased as management reduced the average annual fire extent and frequency at large and medium scales. However, these relationships between fire and richness and abundance were only evident in areas where introduced livestock were removed. This interaction may arise because predation by feral cats is amplified in areas with reduced vegetation ground cover, and cover is reduced over longer periods when livestock have access to burnt areas, because they selectively graze regenerating grass. Fire management for conservation receives substantial investment across northern Australia, and in savannas worldwide; this study shows that without appropriate management of other factors, this investment may be ineffective. More broadly, managing single threats to biodiversity may be compromised if interactions between threats are not explicitly considered. This study provides an example of how such interactions can be evaluated for improved biodiversity conservation.

KEYWORDS
feral cats, fire management, fire regimes, grazing impacts, small mammals, threat interactions, tropical savannas

1 | INTRODUCTION

Conservation management largely depends on identifying the threats causing species to decline, then implementing management to abate those threats. Partly because it is most tractable, conservation research and management usually focus on the impacts and management of threats individually. However, threats may interact additively or synergistically (Brook, Sodhi, & Bradshaw, 2008; Didham, Tylianakis, Gemmell, Rand, & Ewers, 2007), sometimes in...
a manner that may not be readily predictable. In many situations, understanding the potential interactions among multiple threats and environmental factors may be necessary to design and implement management actions that can effectively maintain and recover threatened species (Didham et al., 2007).

The world is experiencing massive global extinction rates (Ceballos et al., 2015) and mammals have been a severely affected group (Hoffmann et al., 2011). Over a third of all mammal extinctions over the last few hundred years have occurred in Australia (Woinarski, Burbidge, & Harrison, 2015). The Australian mammal fauna collapsed first in temperate and arid zones; the collapse is now occurring across most of the higher rainfall tropical savannas of northern Australia (Davies et al., 2018; Woinarski et al., 2011; Ziembicki et al., 2015). These extensive and largely unabated declines have mainly been linked to a suite of land use, ownership, and management changes, resulting in shifts towards more frequent, extensive, and high intensity fires (Andersen et al., 2005; Griffiths, Garnett, & Brook, 2015; Lawes et al., 2015b; Legge et al., 2008; Radford, Gibson, Corey, Carnes, & Fairman, 2015; Woinarski et al., 2011); near-pervasive introduction of grazing by introduced livestock (Kutt & Woinarski, 2007; Legge, Kennedy, Lloyd, Murphy, & Fisher, 2011a; Woinarski & Ash, 2002); and predation by feral cats (Davies et al., 2017; Fisher et al., 2014; Frank et al., 2014; Lawes et al., 2015a). However, conservation management that seeks to reduce the individual impacts of fire or grazing have not consistently resulted in faunal recovery (Ziembicki et al., 2015).

Research seeking to identify drivers of biodiversity loss in savannas have mostly focussed on threats individually (Andersen et al., 2005), and often using plots that are much smaller than the scale over which the threats operate (Archibald, Bond, Stock, & Fairbanks, 2005; Fuhlendorf, Engle, Kerby, & Hamilton, 2009; Kutt & Woinarski, 2007). However, considering interactions among threats, and between threats and the environment, may contribute to a greater understanding of the mechanisms behind decline (Doherty, Dickman, Nimmo, & Ritchie, 2015). For example, in northern Australia, feral cats concentrate their hunting in areas affected by intense fires and grazing (McGregor, Legge, Jones, & Johnson, 2014, 2016) because the reduced ground cover in these areas substantially increases their hunting efficiency (McGregor, Legge, Jones, & Johnson, 2015a), leading to declines in small mammal populations (Leahy et al., 2016). Understanding these interactions is critical for designing appropriate conservation management. Reducing cat density, especially in remote landscapes, is extremely challenging. In contrast, intensively managing fire, or removing livestock, may be a cost-effective way to reduce cat impacts (Bowman & Legge, 2016; Doherty et al., 2017).

Although there has been little scrutiny of how fire and grazing impacts interact to influence small mammal populations in tropical savannas, clearly these two landscape-scale disturbances are linked. Livestock may graze selectively in recently burnt areas (Archibald et al., 2005) and heavy grazing reduces fuel loads and thus affects fire behavior and patterns (Bond & Keeley, 2005; Fuhlendorf et al., 2009; Liedloff, Coughenour, Ludwig, & Dyer, 2001; Skroblin, Legge, Webb, & Hunt, 2014). Without understanding how potential interactions affect native species, conservation management of fire or livestock alone may be unintegrated and ineffective.

A recent analysis of extinction risks for Australian birds and mammals predicted additional mammal extinctions in the tropical savannas of northern Australia over the next 20 years, in the absence of improved management (Geyle et al., 2018). To reduce the risks of such further extinctions, restorative management must be designed with an understanding of how threats interact. We have previously shown that mammals in Australia's north-western savannas are adversely affected by the individual effects of livestock (Legge, Kennedy, et al., 2011a), and by frequent, extensive high-intensity fire (Leahy et al., 2016; Legge et al., 2008; Legge, Murphy, Kingswood, Maher, & Swan, 2011b). Here, we use an unusually (at least for Australia) long-term (13 years) and large-scale (9,000 km²) study to examine whether interactions between key threats (fire and livestock) affect the conservation goal of recovery of native small mammal populations. Given that (a) livestock and frequent extensive fire both depress small mammal richness and abundance, and (b) that livestock constrain vegetation recovery after fire, and (c) that vegetation cover reduces cat hunting activity and success (as described above), we predicted that frequent fire plus livestock would result in the worst outcomes for small mammals, and that infrequent fire and livestock absence would result in the best outcomes. This study relates to the need to improve management effectiveness in relation to a major conservation challenge operating at a semi-continental scale, but the rationale of this study and the research and analytical approach we describe is likely to be relevant to many other situations globally, where conservation outcomes can be achieved only with management rooted in understanding of the complex interactive web of many co-existing threat factors.

2 | METHODS

2.1 | Study area

The study was carried out at Mornington, Marion Downs and Tableland Wildlife Sanctuaries in the Kimberley, north-
western Australia (17°30’S, 126°06’E). Large parts of these adjoining properties (collectively, 895,000 ha) are now managed for conservation by the Australian Wildlife Conservancy, but previously operated as cattle stations from the 1920s until 2001, 2008, and 2011 respectively. In 2004, they collectively supported approximately 16,000 cattle, feral horses, and donkeys. Successive areas were destocked; by the end of 2015, 11,000 livestock had been removed from over 230,000 ha (Figure 1). Strategic fire management also began from 2004, becoming more extensive and successful from 2007, that reduced the annual extent, intensity and frequency of fires (Legge, Murphy, et al., 2011b).

The vegetation of the study site mostly comprises tropical savanna woodlands with a sparse tree layer over a grassy understory of perennial and annual grasses (“woodland”). Most substrates are sandstone or sandstone-derived, with smaller areas of soil of volcanic origin. The dominant savanna woodlands are interspersed with blacksoil grasslands with few or no trees on cracking clay soils (“blacksoil”), riparian vegetation on alluvium along creeks and rivers (“riparian”), and strips of relatively dense vegetation at the base of King Leopold sandstone ranges (“sand-seep”). Rainfall varies from an annual mean of about 700 mm in the south to about 950 mm in the north.

The small mammal fauna sampled in the study area comprise native rodents from four genera and marsupials including one bandicoot species and four dasyurids (Table S2).

### 2.2 Sampling design

To test the individual and interactive impacts of fire and grazing, a series of small permanent plots replicating all combinations of levels of the two main factors of fire and grazing may represent traditional and optimal experimental design (e.g., Woinarski, Brock, Fisher, Milne, & Oliver, 1999). However, the threats from fire and grazing operate over large spatial scales, and unanticipated fire in this environment can readily subvert design at fixed experimental

---

**FIGURE 1** The study area, showing sampling sites coded by habitat, the stocked and destocked areas (with the year each area was destocked in text), and areas that only support very low densities, or no cattle. Major waterways, strategic fencing, and property boundaries are also shown. The location of the study area is indicated by the inset in the top right of the map.
plots (Andersen, Cook, & Williams, 2003). Moreover, we were specifically seeking conservation outcomes from management interventions implemented at landscape-scale across a heterogenous environment. Destocking was implemented across 2,300 km$^2$ of the 9,000 km$^2$ study area, and fire was managed in a regional program covering over 40,000 km$^2$, including the study area.

We used a quasi-experimental design and a matched control/comparison approach (Margoluis, Stem, Salafsky, & Brown, 2009). Sampling occurred over 13 years (2004–2016). Each year, we selected sites in each of the four habitats (woodlands, blacksoil, riparian, sandseep) within destocked areas, matched with sites in similar habitats within stocked areas. For each combination of habitat and stocking status (in any 1 year), we sampled sites across a range of fire regimes, from a regime dominated by frequent extensive and intense fires, to a regime characterized by less frequent, less extensive, and less intense fires. As well as the matching control/comparison design, individual sites acted as their own controls, because the same site could be sampled across different combinations of fire and stocking treatments, over the course of the study. For example, 49 sites progressed from being stocked to becoming destocked, and all sites experienced temporal variation in fire regime. Having sites that moved between stocking status categories, and fire regimes, helped reduce the potential for factors related to a site’s spatial location to confound results.

We used a rotating sampling design, subsampling an average of 60 sites each year from the total set of 186 sites (Figure 1). Compared to resurveying the same set of sites every year, the subsampling approach allowed us to achieve greater spatial coverage, and to sample in a reasonably balanced way across the range of fire regimes, stocking status and habitats (Lindenmayer et al., 2012). Over the course of the study (2004–2016), each of the 186 sites was sampled between 1 and 12 times; both the median and mean number of times that a site was resampled was 4. The average number of sites sampled in a year for every combination of habitat and stocking status was 8. Over the 13-year study, the total number of samples was 783, split between stocked ($n = 383$) and destocked ($n = 400$) treatments. Livestock densities were low to average for the region, at densities of 1.8 livestock/km$^2$ when the study began in 2004 (long-term average for bioregion from 1992 to 2011 = 2.6 dry cows/km$^2$, where dry cows are one of the standard units used to describe stock density, Bastin, 2012). The density of the largest native grazers (Macropus robustus and M. antilopinus) in this region is low (averaging 0.14 and 1.75 animals/km$^2$ respectively, Ritchie, Martin, Krockenberger, Garnett, & Johnson, 2008) and across north Australia the biomass of introduced mammalian herbivores now far exceeds that of native mammalian herbivores (Woinarski, 2014).

### 2.3 Field methods

We sampled the terrestrial small mammal fauna annually during the dry season (May–August). Fauna survey methods were based on the protocol described in (Legge, Kennedy, et al., 2011a). Each site was a 0.25 ha quadrat, with four cage traps, 20 Elliott traps, eight pitfall traps and eight funnel traps. Sites in the same habitat, sampled in the same year, were a minimum of 500 m apart; the average distance between sampled sites was much greater. Sites were operated for a 72-hr period (a “site-sample”), with traps checked at dawn and dusk. For every mammal captured, we noted the species and whether the individual was a recapture (captured mammals were fur-clipped to allow us to distinguish recaptures). This sampling regime provides no information on larger native mammals (e.g., macropods) or bats; and we note that, other than livestock (cattle, horses, donkeys) and feral cats, no other introduced mammals are present in the study area.

### 2.4 Fire regime characterization

For each site on each sampling occasion, we described the fire regime over the preceding 9 years, at three spatial scales, and discriminating between fires of different intensity. Fire spatial data covering 2000–2016 was sourced from MODIS satellite imagery analysis (available from Bushfires NT; www.firenorth.org.au); and for 1995–1999 from the NOAA-AVHRR satellite imagery (interpreted by Department of Land Information; www.landgate.wa.gov.au). Using ARCMap 10.5.1 and Python scripts, we converted the satellite imagery data to 100 m raster format. Every raster cell was categorized as burnt or unburnt; fires were further classified as “early” if they occurred between January and June (covering the wet and early dry seasons), and as “late” if they occurred between July and December (the late dry season). “All” fire referred to both early and late fires combined. In our study area, the end of June marks a switch from fires that are mostly prescribed, of low intensity, and small extent, to fires that are unmanaged (wildfires), of higher intensity, and greater extent (Legge, Murphy, et al., 2011b). Since sites were sampled mid-year, year was defined as the preceding 12 months (i.e., year 2012 included the second half of 2011 and the first half of 2012).

We described fire regimes at three spatial scales chosen to correspond with the home range of mammals (site scale, 1 ha) (Leahy et al., 2016); with a small population of small mammals (medium scale, 1 km$^2$); and with the scale at which threats operate in this landscape (stock mostly walk up to 5 km back and forth from water, cats have home ranges of 3–5 km across, and unmanaged fires easily traverse 10 km and more, Legge, Murphy, et al., 2011b; Hunt,
McIvor, Grice, & Bray, 2014; McGregor, Legge, Potts, Jones, & Johnson, 2015b) (large scale, 100 km²).

The site scale fire frequency was calculated as the average number of times the sampling site was burnt (in early, late, and all fires) in the preceding 9 years. To generate fire metrics at medium and large scales, the sampling site was positioned centrally in the scale area, and we calculated the percentage of raster cells in the scale area that were burnt early, burnt late, or burnt regardless of season (all), in the year preceding the fauna sample. We averaged the percentages burnt each year (for early, late and all fires), over the preceding 9 years, to generate a metric for “fire prevalence.”

We use the term fire prevalence rather than annual fire extent because the metric contains information on both the area burnt each year as well as fire frequency. Sample areas with the highest values will be those that frequently have a large percentage burnt annually; sample areas with the lowest values will be those with infrequent and small annual burns. Sample areas with middle-range values could represent areas that burn infrequently with large fires, or areas that experience burns more frequently, but where the burnt areas are relatively small.

Since fire regimes were described in terms of their frequency at the site, and their prevalence at two spatial scales (medium and large), with fires (all fire) also distinguished by their intensity (early vs. late), this resulted in nine different fire regime variables.

2.5 | Analysis

We summed the total number of species caught at a site (richness), and the total number of individuals of all species (i.e., excluding recaptures) captured at that site (abundance) during a sampling session. We examined variation in richness and abundance against habitat, stocking status, and fire variables, using R (version 3.2.4, R Core Team, 2016). Year and site were specified as random terms in the models. For mammal richness, we fitted generalized linear mixed models with Poisson error distributions using the package lme4 (Bates, Maechler, & Bolker, 2017). The data for abundance were overdispersed, so we fitted generalized linear mixed models with negative binomial error distributions and log link functions using the package lme4 (Bates, Maechler, & Bolker, 2017). Preliminary exploratory analysis confirmed that the fire variables are closely correlated. To simplify analyses we therefore used the variables for late fire, plus those for all fires. To avoid residual problems with co-linearity between fire variables in the same model, we only fitted one fire variable (with its interactions with other terms) in each candidate model. For both abundance and richness analyses, we constructed a set of 82 candidate models, comprising all combinations of the main effects habitat, stocking status, one fire variable, and their two and three-way interactions (with year and site as random terms in each case), plus the null model. We evaluated models using the bias-corrected form of Akaike’s Information Criterion (AICc) and Akaike weight (w_i) (Burnham & Anderson, 2003). We considered models to be top-ranked where ΔAICc was <2. If more than one model was supported, we used a model averaging approach to generate parameter estimates based on conditional model-averaged coefficients obtained from summed Akaike weights (Burnham & Anderson, 2003). We also assessed the relative importance of predictor variables in top-ranked models using w+, which is the sum of Akaike weights for all models containing a given predictor variable (Burnham & Anderson, 2003). Exploration of predicted values from interacting variables was carried out for fixed effects using the Effects package (Fox, 2003) in program R.

We investigated whether individual species responded to fire and livestock in similar ways. Some individual species were captured in very low numbers overall, with captures at site-samples mostly being zero. We excluded species that were detected at fewer than 5% of site-samples (i.e., 39 of the total 783 site-samples). This excluded Pseudantechinus nyingbing, Sminthopsis macroura, Isoodon macrourus, Zyzomys argurus, and Leggadina lakedownensis. For the remaining five species, we used a generalized mixed model with a binomial error distribution to examine whether, for each species, their detection (yes/no) at site-samples was similarly influenced by fire and grazing. We fitted the variables from the top-ranked model from the analysis of overall mammal abundance, but this time we interacted those variables with species. The random model included year and site. We used Wald statistics to assess the influence of each fixed effect.

3 | RESULTS

Fire regimes were similar across habitats: on average sites burned 2.5 times in 9 years (or once every 3.6 years); the average fire prevalence in the 1 km × 1 km area surrounding a site was 28%, and in the 10 km × 10 km area surrounding a site it was 29% (Table S1). Overall, we caught 2304 individuals from 10 species (five rodents, five marsupials) (Table S2). Capture rates varied among individual species and habitats, with highest capture rates for Rattus tunneyi (884 individuals) and sandseep habitat (806 mammal captures). Captures of each species also varied among habitats, ranging from a mean of 2.46 R. tunneyi individuals per site-sample in sandseep habitat, to a mean of zero individuals per site-sample for eight species-habitat combinations (Table S2).

In the mammal richness analysis, only one model had ΔAICc <2; for mammal abundance, there were two models...
Mammal richness increased as the prevalence of late fires at the large scale (10 km × 10 km around the sample site) decreased (Table 1). Mammal abundance increased as the fire prevalence of all fires (i.e., regardless on intensity) at the medium scale (1 km × 1 km around the sampling site) decreased (Table 1). Richness and abundance were higher in sandseep than other habitats (Tables S3 and S4).

The relationship between both mammal richness and abundance to fire regimes depended on stocking status. Richness increased as fire prevalence decreased, but only at destocked sites (Table 1 and Figure 2), where richness increased by about one third of a species for every reduction in late fire prevalence of 10% (Table S3). Abundance also increased as the fire prevalence decreased, again only at destocked sites (Table 1 and Figure 3a); where abundance increased by about one fifth of an animal for every reduction of 10% in fire prevalence (Table S4). Mammal abundance was also influenced by the interaction between habitat and stocking status (Table 1): abundance was higher at destocked sites in blacksoil, riparian, and sandseep habitats, but the effect of destocking was less evident in woodland habitats (Figure 3b). The habitat-stocking status interaction was a less important variable than others in the top-ranked models (Table S5).

Of the five more commonly captured species, the abundance of four species showed similar relationships to fire and grazing: *Planigale ingrami*, *Planigale maculata*, *Pseudomys nanus* and *R. tunneyi* were detected more often at destocked sites (Figure 4a), and as fire prevalence at the medium scale decreased (Figure 4b). *Pseudomys delicatulus* showed opposite patterns—it was commonly detected at

Table 1. Model ranking results for the analysis of (a) mammal species richness, and (b) mammal abundance

| (a) Richness: Top 10 candidate models | Log (l) | K | AICc | ΔAICc | wi |
|-------------------------------------|--------|---|------|-------|----|
| Habitat + stocking status * late-fire-large | −982.9 | 7 | 1980 | 0.000 | 0.342 |
| Stocking status * late-fire-large + habitat * late-fire-large | −980.8 | 10 | 1982 | 2.052 | 0.123 |
| Stocking status * late-fire-large + habitat * late-fire-large + habitat * stocking status | −977.8 | 13 | 1982 | 2.057 | 0.122 |
| Habitat * late-fire-large * stocking status | −975.1 | 16 | 1983 | 2.962 | 0.078 |
| Habitat * all-fire-large * stocking status | −975.7 | 16 | 1984 | 4.224 | 0.041 |
| Habitat * stocking status + habitat * all-fire-medium + stocking status * all-fire-medium | −979.0 | 13 | 1984 | 4.513 | 0.036 |
| Habitat * stocking status + all-fire-medium | −976.3 | 16 | 1985 | 5.454 | 0.022 |
| Habitat * stocking status | −984.6 | 8 | 1985 | 5.540 | 0.021 |
| Habitat * stocking status + all-fire-medium | −980.6 | 12 | 1986 | 5.763 | 0.019 |
| Habitat * stocking status + all-fire-large | −980.7 | 12 | 1986 | 5.973 | 0.017 |

| (b) Abundance: Top 10 candidate model | Log (l) | K | AICc | ΔAICc | wi |
|--------------------------------------|--------|---|------|-------|----|
| Stocking status * habitat + stocking status * all-fire-medium | −1,560 | 13 | 3,147 | 0.000 | 0.400 |
| Habitat + stocking status * all-fire-medium | −1,564 | 10 | 3,149 | 1.741 | 0.168 |
| Stocking status * habitat + all-fire-large | −1,562 | 13 | 3,150 | 2.953 | 0.091 |
| Stocking status * habitat + all-fire-medium + habitat + all-fire-medium | −1,559 | 16 | 3,151 | 3.835 | 0.059 |
| Habitat * stocking status * all-fire-large | −1,556 | 19 | 3,152 | 4.883 | 0.035 |
| Habitat * late-fire-large + stocking status * late-fire-large | −1,563 | 13 | 3,152 | 4.897 | 0.035 |
| Habitat * stocking status + stocking status * late-fire-large | −1,560 | 16 | 3,152 | 5.223 | 0.029 |
| Habitat * stocking status * all-fire-med | −1,557 | 19 | 3,152 | 5.582 | 0.025 |
| Habitat * all-fire-med + stocking status * all-fire-med | −1,563 | 13 | 3,153 | 5.955 | 0.020 |
| Habitat * stocking status + stocking status * fire-site | −1,563 | 13 | 3,153 | 5.979 | 0.020 |

Table presents the top 10 models in each analysis. Fire refers to fire frequency (at site scale) or fire prevalence (at medium or large scales), calculated for late fire or all fire. Models with interaction terms (*) also contain the constituent main effects and any subsidiary second-order interaction terms if the model contains a three-way interaction. All models contain the random terms year and site. The models are in ascending order of the second-order model selection criterion of Akaike's information criterion (AICc). Log(l) is the maximized log-likelihood of the model; K is the number of estimated parameters including the intercept; AICc is the selection criterion; ΔAICc is the difference between the model's AICc value and the minimum AICc value; and wi is the Akaike weight. All models are ranked according to support, thus ΔAICc = 0 for the best model, with some support also (ΔAICc < 2) for the second ranked model in the abundance analysis (bold type).
stocked sites (Figure 4a) and at sites with a higher fire prevalence (Figure 4b) (Interaction between species and stocking status: $\chi^2 = 43.6; p < 0.001$; interaction between species and fire prevalence: $[\chi^2 = 27.6; p < 0.001]$). The interaction between fire and grazing highlighted in the overall model for mammal abundance was also significant ($X^2 = 9.36; p < 0.01$), but the nature of this interaction did not significantly differ between species (three-way interaction between species, fire prevalence and stocking status: $X^2 = 1.50; p = 0.83$) (Table S6).

## 4 | DISCUSSION

This long-term and landscape-scale (13 years, 9,000 km²) study of mammal populations exposed to varying combinations of livestock and fire regimes in the tropical savannas of north Australia demonstrates the importance of understanding the interactions between threats when implementing conservation management. Four key results emerge from the analyses. First, small mammal populations responded most strongly to fire regimes in a relatively large area around the sampling point. Second, mammal richness and abundance increased as the prevalence of fire decreased. Third, mammal abundance was more strongly affected by the prevalence of any fires, than solely by high intensity fires. Fourth, the effect of fire interacted with the presence of another threat (livestock). Below, we discuss and seek to explain the relationship between fire regimes and mammals; the interactions between fire and livestock and the implications of interacting threats for conservation management.

### 4.1 | Fire regimes that affect mammals

Increased fire prevalence could affect mammal populations in a variety of ways: in the short term, fire removes grass cover (exposing small mammals to greater predation risk; Leahy et al., 2016), and removes food resources including grass seed and grass stems (Andersen et al., 2005). If fire recurs frequently, key food plants are disadvantaged,
including fleshy fruited shrubs, flowers, and some grasses (Atchison, 2009; Connor et al., 2017). The abundance of shelter sites such as hollow logs and tree hollows are also reduced by high intensity fire, especially if these fires recur frequently (Firth, Woinarski, Brennan, & Hempel, 2006; Williams, Cook, Gill, & Moore, 1999; Woolley, Murphy, Radford, Westaway, & Woinarski, 2018).

In this study, fire regimes were most influential when considered at scales much larger (i.e., from 1 km × 1 km; to 10 km × 10 km) than the home ranges of the individual mammals (see also Lawes, et al., 2015b; Pastro, Dickman, & Letnic, 2011). This suggests that the population status at a sampling site depends on processes, such as predation and source–sink dynamics, operating at larger scales. In Australia’s northern savannas, fire generally does not directly kill individual mammals, but reduces individual survivorship and causes population decline for some species in the weeks following the fire (Begg, Martin, & Price, 1981; Leahy et al., 2016; Legge et al., 2008). Population recovery at burnt sites post-fire could occur though dispersal from neighboring unburnt areas, reproduction by surviving individuals within the burnt area, or both. If fires burn extensively and mammal populations are reduced over large areas, there will be little dispersal (at least in the short term) from unburnt areas to recolonize sites within the fire footprint (Griffiths & Brook, 2015). The species encountered in the study have generation lengths of between 1 and 3 years (http://www.iucnredlist.org/). On average, sites were burnt every 3 years. Thus, in current average conditions, every generation of mammal is experiencing about one fire event in their lifetime, and the reduced survivorship associated with that. It follows that frequent, extensive fire must be the worst scenario, with mammal populations held at suppressed densities over large areas, and population recovery via reproduction and dispersal both constrained (Woinarski, Williams, Price, & Rankmore, 2005).

At destocked sites, mammal richness and abundance were greatest at lowest values of fire prevalence. Low fire prevalence could arise from low-moderate frequencies of small fires, or a very low frequency of extensive fire. In either scenario, patches of relatively long-unburnt (in this situation, 3+ years) vegetation will be present, but shift spatially and temporally. Empirical results and modelling predictions from other work also point to the importance of long-unburnt vegetation and fire frequencies of less than one fire every 4–5 years for maintaining small mammal communities (Firth, Brook, Woinarski, & Fordham, 2010; Griffiths et al., 2015; Radford et al., 2015). However, the prevailing fire frequencies across north Australia are generally higher than this (with fires every 1–3 years), highlighting a broad-scale operational challenge to achieving fire management that can maintain or recover populations of small mammals (Legge, Murphy, et al., 2011b; Yates, Edwards, & Russell-Smith, 2009).

Species richness was most responsive to the prevalence of high intensity fires, whereas abundance was most influenced by the prevalence of any fires, irrespective of fire intensity. These patterns broadly align with previous research that shows mammal populations are affected by the incidence of extensive fire, mostly irrespective of fire intensity, although high intensity fires appear more detrimental in some studies (Andersen et al., 2005; Firth et al., 2010; Perry, Vanderduys, & Kutt, 2015; Radford et al., 2015; Woinarski et al., 2011). With repeated late (i.e., more intense) fires, the
densities of rarer mammal species may be reduced to the point where they are not detected during a sampling survey, whereas more common species are still caught, but in lower numbers. Thus, late fires could potentially affect species richness more strongly than abundance. The prevalence of all fires appears as a variable in five of the 10 top-ranked models for mammal richness, and these fire variables are correlated, so the distinction between the impacts from late versus all fires is relatively minor. Species richness was influenced most strongly by the fire regime at large scales (10 km × 10 km), whereas abundance was more influenced by fires at medium scales (1 km × 1 km). Again, the disparity is un compelling: these two fire variables are correlated, and variables of both medium and large scales appeared in the 10 top-ranked models for both richness and abundance.

4.2 | Interactions between fire, grazing and habitat

We predicted that high prevalence of fire plus livestock would result in the worst outcomes for small mammals, and that low fire prevalence in the absence of livestock would result in the best outcomes. This prediction was partly supported: mammal richness and abundance were indeed highest at destocked sites with low fire prevalence. However, mammal richness and abundance were low at stocked sites regardless of the fire regime, and low at sites with high fire prevalence regardless of the stocking status (Figure 5). This suggests that livestock and fire impacts interact synergistically rather than additively: as the prevalence of fire around sampling sites decreased, both mammal richness and abundance increased. However, this increase was only evident at destocked sites; in the presence of livestock, this recovery was not realized. A comparable interaction was also reported for one mammal species in the only similar study elsewhere in northern Australia, where populations of Pseudomys desertor populations recovered more rapidly post-fire at sites that were ungrazed relative to sites that were grazed (Kutt & Woinarski, 2007).

Why should the presence of livestock neutralize the potential benefits of reduced fire prevalence? In this savanna environment, managers typically reduce the frequency of extensive fires in the late dry season by strategically burning small areas during the early dry season. These prescribed burns limit the spread of fires later in the dry season and enhance the ability of managers to extinguish unmanaged fires. Typically, there is partial but rapid recovery of grass and ground-shrub cover after the prescribed fires, driven by residual moisture in the soil, seasonal dews and sometimes late showers. This partial recovery re-establishes some post fire cover for small mammals. However, where present, livestock are attracted to the regenerating vegetation in the burnt areas and graze it to the ground (Bond & Keeley, 2005; Hunt et al., 2014; Liedloff et al., 2001). This preference occurs because grasses in adjacent unburnt areas are typically cured and of low nutritive value (Ash, McIvor, Mott, & Andrew, 1997). Hence, in the presence of livestock, burnt areas remain bare until the next wet season, up to 8 months later. Given that open areas also attract feral cats, even from kilometres away (McGregor et al., 2016), a prescribed burn that is grazed by livestock could act as a sink for native mammals, thus neutralizing the otherwise positive impacts of reducing fire frequencies at a large scale (Figure 5). Some native grazers may also be attracted to recently burnt areas (Ritchie et al., 2008), but given they exist at much lower biomass than introduced species (Woinarski, 2014), the impacts of their grazing are likely far less.

An alternative explanation is that the combination of fire and grazing reduces food resources for small mammals that rely on grass seeds and grass stems. If this were true, we should see a greater response to livestock removal and reduced fire prevalence from the granivorous and herbivorous rodents, rather than the insectivorous dasyurids and generalist bandicoot. However, opposite to this prediction, the rodents were similarly or less sensitive to livestock presence than the dasyurids and tended to be detected at sites with fire prevalence values greater than at sites with dasyurid detections (Figure 4b).

With the exception of P. delicatulus, species responded consistently to variation in livestock presence and fire prevalence. P. delicatulus, contra other species, had a higher detection rate at stocked sites, and was detected at sites with higher fire prevalence. Previous studies have likewise found this mouse to be relatively resilient to fire and grazing impacts (Davies et al., 2018; Kutt & Woinarski, 2007; Legge et al., 2008), possibly because it has very high fecundity (including continuous breeding), broad diet and habitat tolerance, and because its burrow systems provide some shelter from fire and predation (Braithwaite & Brady, 1993).

We note that livestock grazing may reduce grass fuel loads, and therefore also reduce the intensity and possibly even the prevalence of fire. However, in this study, high levels of grazing were evident only in very small areas (i.e., <10 ha) and not at scales large enough to affect fire regimes. For example, the average fire prevalence in both woodland and riparian habitats was similar (30%; Table S1), even though woodland was the least preferred habitat for cattle, and riparian among the most preferred.

4.3 | Management implications

Our results corroborate the observation that populations of small mammals in Australia's northern tropical savannas are fire-sensitive, and that strategic and systematic prescribed
burning must aim to reduce the extent and frequency of fire, and increase the overall extent of relatively long-unburnt vegetation, beyond the current norm. In this system, that means reducing frequencies to less than 1 year in four or five, as recommended on the basis of compelling evidence, from this and many previous studies (Andersen et al., 2005; Firth et al., 2010; Lawes, et al., 2015b; Perry et al., 2015; Radford et al., 2015; Woinarski et al., 2011; Woinarski & Legge, 2013; Ziembicki et al., 2015). However, this conservation ideal still remains little realized, even on conservation reserves (Woinarski & Wind-erlich, 2014).

Even if fire management successfully reduces fire extent and frequency, it may be ineffective for the recovery of the region's mammal fauna: we found that co-management of fire and livestock is required to support population recovery of small mammals. Unburnt areas are shown by the grass background; lightest gray shows areas that have been burnt but have high grass regeneration. Darkest grey indicates areas with little or no post-fire grass cover (due to intense fire, grazing, or both).

Even if fire management successfully reduces fire extent and frequency, it may be ineffective for the recovery of the region's mammal fauna: we found that co-management of fire and livestock is required to support population recovery of small mammals. Unburnt areas are shown by the grass background; lightest gray shows areas that have been burnt but have high grass regeneration. Darkest grey indicates areas with little or no post-fire grass cover (due to intense fire, grazing, or both). Values were before the threats of fire, livestock and feral cats began to take effect. In addition, several mammal species (e.g., golden bandicoot Isoodon auratus, golden-backed tree-rat Mesembriomys macrurus) that were extirpated from the region following pastoral settlement (Kitchener, 1978; McKenzie, 1981; Start, Burbidge, McKenzie, & Palmer, 2007) remain absent despite over a decade of conservation management. It is possible they are prevented from recolonizing the study area from the nearest relic populations by areas of land where threats are inadequately managed.

Across the tropical savannas of north Australia, there is considerable investment in fire management, mostly for greenhouse gas emissions abatement and conservation purposes. Our results strongly suggest that the efficacy of this investment for small mammal recovery depends on whether or not livestock are present, as well as the presence of other threats like feral cats. Yet, livestock (and cats) are almost ubiquitous across northern Australia, absent from only the most topographically rugged areas, some islands and some small areas where intensive effort has been made to remove them (Legge et al., 2018; Woinarski, 2014), suggesting that some of the current investment in fire management will be ineffective for conservation.

**FIGURE 5** A schematic diagram showing the effects of different combinations of fire prevalence and stocking status on the relative availability of cover from post-fire grass regeneration (represented by the grass tuft symbols), the relative activity and predation pressure from cats, and the resulting numbers of small mammals. Unburnt areas are shown by the grass background; lightest gray shows areas that have been burnt but have high grass regeneration. Darkest grey indicates areas with little or no post-fire grass cover (due to intense fire, grazing, or both).
Globally, there are many situations where the recovery of declining biodiversity is not being achieved, despite dedicated investment in the management of a major threat. In the example here, we show that such failures may be because of interactions among threatening factors, and that evidence arising from large-scale, long-term research that can pick apart the individual and interactive influence of multiple factors may be a necessary basis for understanding the complex threat environment, finessing management direction and improving conservation outcomes.

ACKNOWLEDGMENTS

This study was funded by Australian Wildlife Conservancy supporters and grants, including from The Nature Conservancy's David Thomas Challenge; the Western Australian Government's Kimberley Science and Conservation Strategy; the Australian Government's National Environmental Research Program, and the Caring For Our Country Program. During manuscript preparation, S.L. and J.W. were supported by the Australian government's National Environmental Science Program's Threatened Species Recovery Hub; K.T. was supported by the Arid Recovery project. We thank Bill Venables and Leigh-Ann Woolley for assistance with analysis, and John Kanowski for comments. Fieldwork was conducted by many AWC staff, interns, volunteers; in particular, Joanne Heathcote, Malcolm Kennedy, Richard Kingswood, Julie Kingswood, Ray Lloyd, Hugh McGregor, Kim Maute, Danae Moore, Andrew Morton, Eridani Mulder, Steve Murphy, Doug Schaefer, Anja Skroblin, Dan Swan and Toby Barton made considerable contributions to this project.

CONFLICT OF INTEREST

The authors declare no potential conflicts of interest.

AUTHOR CONTRIBUTIONS

All authors contributed to research design, interpreting data, and writing the manuscript. S.L., J.S., A.S., and K.T. organized and led the field data collection; S.L., J.S., and T.W. carried out the analyses; S.L. led the manuscript preparation, to which all authors contributed.

DATA ACCESSIBILITY

Data are accessible on figshare doi: 10.6084/m9.figshare.8100149.

ETHICS STATEMENT

Animal trapping was carried out under ethics permits and fauna licences from the Western Australian government's Department of Biodiversity, Conservation and Attractions; plus Animal Use and Supply permits from the Western Australian government's Department of Agriculture and Food.

ORCID

Sarah Legge https://orcid.org/0000-0001-6968-2781

REFERENCES

Andersen, A. N., Cook, G. D., Corbett, L. K., Douglas, M. M., Eager, R. W., Russell-Smith, J., … Woinarski, J. C. Z. (2005). Fire frequency and biodiversity conservation in Australian tropical savannas: Implications from the Kapalga fire experiment. Austral Ecology, 30, 155–167.

Andersen, A. N., Cook, G. D., & Williams, R. J. (Eds.). (2003). Fire in tropical savannas: The Kapalga experiment. New York: Springer-Verlag.

Archibald, S., Bond, W. J., Stock, W. D., & Fairbanks, D. H. K. (2005). Shaping the landscape: Fire–grazer interactions in an African savanna. Ecological Applications, 15, 96–109.

Ash, A. J., McVor, J. G., Mott, J. J., & Andrew, M. H. (1997). Building grass castles: Integrating ecology and management of Australia’s tropical tallgrass rangelands. Rangeland Journal, 19, 123–144.

Atchison, J. (2009). Human impacts on Persoonia falcata. Perspectives on post-contact vegetation change in Keep River region, Australia, from contemporary vegetation surveys. Vegetation History and Archaeobotany, 18, 147–157.

Bastin, G. (2012). ACRIS livestock density update 2009–2011. Canberra: ACRIS Management Unit Department of Environment.

Bates, D., Maechler, M., & Bolker, B. (2011). lme4: Linear mixed-effects models using S4 classes. R package version 0999938-35. Retrieved from http://CRAN.R-project.org/package=lme4

Begg, R. J., Martin, K. C., & Price, N. F. (1981). The small mammals of Little Nourlangie Rock, N.T. V. The effects of fire. Australian Wildlife Research, 8, 515–527.

Bolker, B., Skaug, H., & Laake, J. (2017). Package ‘R2admb’: ‘ADMB’ to R interface functions, version 0.7.16. Retrieved from ftp://mandriva.c3sl.ufpr.br/CRAN/web/packages/R2admb/R2admb.pdf

Bond, W. J., & Keeley, J. E. (2005). Fire as a global ‘herbivore’: The ecology and evolution of flammable ecosystems. Trends in Ecology & Evolution, 20, 387–394.

Braithwaite, R. W., & Brady, P. (1993). The delicate mouse, Pseudomys delicatulus: A continuous breeder waiting for the good times. Australian Mammalogy, 16, 94–98.

Brook, B. W., Sodhi, N. S., & Bradshaw, C. J. A. (2008). Synergies among extinction drivers under global change. Trends in Ecology & Evolution, 23, 453–460.
Burnham, K. P., & Anderson, D. R. (2003). *Model selection and multi-model inference: A practical information-theoretic approach*. New York: Springer.

Ceballos, G., Ehrlich, P. R., Barnosky, A. D., García, A., Pringle, R. M., & Palmer, T. (2015). Accelerated modern human-induced species losses: Entering the sixth mass extinction. *Science Advances*, 1(5), e1400253.

Connor, S. E., Schneider, L., Trezise, J., Rule, S., Barrett, R. L., Zawadzki, A., & Haberle, S. G. (2017). Forgotten impacts of European land-use on riparian and savanna vegetation in North-Western Australia. *Journal of Vegetation Science*, 29, 427–437.

Davies, H. F., McCarthy, M. A., Firth, R. S. C., Woinarski, J. C. Z., Gillespie, G. R., Andersen, A. N., … Murphy, B. P. (2017). Top-down control of species distributions: Feral cats driving the regional extinction of a threatened rodent in northern Australia. *Diversity and Distributions*, 23, 272–283.

Davies, H. F., McCarthy, M. A., Firth, R. S. C., Woinarski, J. C. Z., Gillespie, G. R., Andersen, A. N., … Kerinaiau, C. (2018). Declining populations in one of the last refuges for threatened mammal species in northern Australia. *Austral Ecology*, 43, 602–612.

Didham, R. K., Tylianakis, J. M., Gemmell, N. J., Rand, T. A., & Ewers, R. M. (2007). Interactive effects of habitat modification and species invasion on native species decline. *Trends in Ecology & Evolution*, 22, 489–496.

Doherty, T. S., Dickman, C. R., Johnson, C. N., Legge, S. M., Ritchie, E. G., & Woinarski, J. C. Z. (2017). Impacts and management of feral cats *Felis catus* in Australia. *Mammal Review*, 47, 83–97.

Doherty, T. S., Dickman, C. R., Nimmo, D. G., & Ritchie, E. G. (2015). Multiple threats, or multiplying the threats? Interactions between invasive predators and other ecological disturbances. *Biological Conservation*, 190, 60–68.

Firth, R. S. C., Brook, B. W., Woinarski, J. C. Z., & Fordham, D. A. (2010). Decline and likely extinction of a northern Australian native rodent, the brush-tailed rabbit-rat *Conilurus penicillatus*. *Biological Conservation*, 143, 1193–1201.

Firth, R. S. C., Woinarski, J. C. Z., Brennan, K. G., & Hempel, C. (2006). Environmental relationships of the brush-tailed rabbit-rat, *Conilurus penicillatus*, and other small mammals on the Tiwi Islands, northern Australia. *Journal of Biogeography*, 33, 1820–1837.

Fisher, D. O., Johnson, C. N., Lawes, M. J., Fritz, S. A., McCallum, H., Blomberg, S. P., … Kutt, A. (2014). The current decline of tropical marsupials in Australia: Is history repeating? *Global Ecology and Biogeography*, 23, 181–190.

Fox, J. (2003). Effect displays in R for generalised linear models. *Journal of Statistical Software*, 8, 1–27.

Frank, A. S. K., Johnson, C. N., Potts, J. M., Fisher, A., Lawes, M. J., Woinarski, J. C. Z., … Legge, S. (2014). Experimental evidence that feral cats cause local extirpation of small mammals in Australia's tropical savannas. *Journal of Applied Ecology*, 51, 1486–1493.

Fuhlendorf, S. D., Engle, D. M., Kerby, J., & Hamilton, R. (2009). Pyric herbivory: Rewilding landscapes through the recoupling of fire and grazing. *Conservation Biology*, 23, 588–598.

Geyle, H. M., Woinarski, J. C. Z., Baker, G. B., Dickman, C. R., Dutson, G., Fisher, D. O., … Garnett, S. T. (2018). Anticipating and predicting Australian bird and mammal extinctions. *Pacific Conservation Biology*, 24, 157–167.

Griffiths, A. D., & Brook, B. W. (2015). Fire impacts recruitment more than survival of small-mammals in a tropical savanna. *Ecosphere*, 6, 1–22.

Griffiths, A. D., Garnett, S. T., & Brook, B. W. (2015). Fire frequency matters more than fire size: Testing the pyrodiversity–biodiversity paradigm for at-risk small mammals in an Australian tropical savanna. *Biological Conservation*, 186, 337–346.

Hoffmann, M., Belant, J. L., Chanson, J. S., Cox, N. A., Lamoreux, J., Rodrigues, A. S. L., … Stuart, S. N. (2011). The changing fates of the world's mammals. *Philosophical Transactions of the Royal Society of London B: Biological Sciences*, 366, 2598–2610.

Hunt, L. P., McIvor, J. G., Grice, A. C., & Bray, S. G. (2014). Principles and guidelines for managing cattle grazing in the grazing lands of northern Australia: Stocking rates, pasture resting, prescribed fire, paddock size and water points – A review. *The Rangeland Journal*, 36, 105–119.

Kitchener, D. J. (1978). Mammals of the Ord River area, Kimberley, Western Australia. *Records of the Western Australian Museum*, 6, 189–219.

Kutt, A. S., & Woinarski, J. C. Z. (2007). The effects of grazing and fire on vegetation and the vertebrate assemblage in a tropical savanna woodland in north-eastern Australia. *Journal of Tropical Ecology*, 23, 95–106.

Lawes, M. J., Fisher, D. O., Johnson, C. N., Blomberg, S. P., Frank, A. S. K., Fritz, S. A., … Kutt, A. (2015a). Correlates of recent declines of rodents in northern and southern Australia: Habitat structure is critical. *PLoS One*, 10, e0130626.

Lawes, M. J., Murphy, B. P., Fisher, A., Woinarski, J. C. Z., Edwards, A. C., & Russell-Smith, J. (2015b). Small mammals decline with increasing fire extent in northern Australia: Evidence from long-term monitoring in Kakadu National Park. *International Journal of Wildland Fire*, 24, 712–722.

Leahy, L., Legge, S., Tuft, K., McGregor, H. W., Barmuta, L. A., Jones, M. E., & Johnson, C. N. (2016). Amplified predation after fire suppresses rodent populations in Australia's tropical savannas. *Wildlife Research*, 42, 705–716.

Legge, S., Kennedy, M., Lloyd, R., Murphy, S., & Fisher, A. (2011a). Rapid recovery of mammal fauna in the central Kimberley, northern Australia, following the removal of introduced herbivores. *Austral Ecology*, 36, 791–799.

Legge, S., Murphy, S., Heathcote, J., Flaxman, E., Augustyn, J., & Crossman, M. (2008). The short-term effects of an extensive and high-intensity fire on vertebrates in the tropical savannas of the central Kimberley, northern Australia. *Wildlife Research*, 35, 33–43.

Legge, S., Murphy, S., Kingswood, R., Maher, B., & Swan, D. (2011b). EcoFire: Restoring the biodiversity values of the Kimberley region by managing fire. *Ecological Management and Restoration*, 12, 84–92.

Legge, S., Woinarski, J. C. Z., Burbidge, A. A., Palmer, R., Ringma, J., Mitchell, N., … Tuft, K. (2018). Havens for threatened Australian mammals: The contributions of fenced areas and offshore islands to protecting mammal species that are susceptible to introduced predators. *Wildlife Research*, 45, 627–644.

Liedloff, A. C., Coughenour, M. B., Ludwig, J. A., & Dyer, R. (2001). Modelling the trade-off between fire and grazing in a tropical savanna landscape, northern Australia. *Environment International*, 27, 173–180.

Lindenmayer, D. B., Zammit, C., Attwood, S. J., Burns, E., Shepherd, C. L., Kay, G., & Wood, J. (2012). A novel and cost-effective monitoring approach for outcomes in an Australian biodiversity conservation incentive program. *PLoS One*, 7, e50872.
Margoluis, R., Stem, C., Salafsky, N., & Brown, M. (2009). Design alternatives for evaluating the impact of conservation projects. *New Directions for Evaluation, 2009*, 85–96.

McGregor, H. W., Legge, S., Jones, M. E., & Johnson, C. N. (2014). Landscape management of fire and grazing regimes alters the fine-scale habitat utilisation by feral cats. *PLOS One, 9*, e90997.

McGregor, H. W., Legge, S., Jones, M. E., & Johnson, C. N. (2015a). Feral cats are better killers in open habitats, revealed by animal-borne video. *PLOS One, 10*, e0133915.

McGregor, H. W., Legge, S., Jones, M. E., & Johnson, C. N. (2015b). Density and home range of feral cats in north-western Australia. *Wildlife Research, 42*, 223–231.

Mckenzie, N. L. (1981). Mammals of the Phanerozoic south-west Kimberley, Western Australia: Biogeography and recent changes. *Journal of Biogeography, 8*, 263–280.

Pastro, L. A., Dickman, C. R., & Letnic, M. (2011). Burning for biodiversity or burning biodiversity? Prescribed burn vs. wildfire impacts on plants, lizards, and mammals. *Ecological Applications, 21*, 3238–3253.

Perry, J. J., Vanderduys, E. P., & Kutt, A. S. (2015). More famine than feast: Pattern and variation in a potentially degenerating mammal fauna on Cape York Peninsula. *Wildlife Research, 42*, 475–487.

R Core Team. (2016). *R: A language and environment for statistical computing [computer software]*. Vienna: R Foundation for Statistical Computing.

Radford, I. J., Gibson, L. A., Corey, B., Carnes, K., & Fairman, R. (2015). Influence of fire mosaics, habitat characteristics and cattle disturbance on mammals in fire-prone savanna landscapes of the northern Kimberley. *PLOS One, 10*, e0130721.

Ritchie, E. G., Martin, J. K., Krockenberger, A. K., Garnett, S., & Johnson, C. N. (2008). Large herbivore distribution and abundance: Intra- and interspecific niche variation in the tropics. *Ecological Monographs, 78*, 105–122.

Skroblin, A., Legge, S., Webb, T., & Hunt, L. P. (2014). EcoFire: Regional-scale prescribed burning increases the annual carrying capacity of livestock on pastoral properties by reducing pasture loss from wildfire. *The Rangeland Journal, 36*, 133–142.

Start, A. N., Burbidge, A. A., McKenzie, N. L., & Palmer, C. (2007). The status of mammals in the North Kimberley, Western Australia. *Australian Mammalogy, 29*(1), 16.

Williams, M. A. J., Cook, G. D., Gill, A. M., & Moore, P. H. R. (1999). Fire regime, fire intensity and tree survival in a tropical savanna in northern Australia. *Australian Journal of Ecology, 24*, 50–59.

Woinarski, J. C. Z. (2014). The illusion of nature: Perception and the reality of natural landscapes, as illustrated by vertebrate fauna in the Northern Territory, Australia. *Ecological Management & Restoration, 15*, 30–33.

Woinarski, J. C. Z., & Ash, A. J. (2002). Responses of vertebrates to pastoralism, military land use and landscape position in an Australian tropical savanna. *Austral Ecology, 27*, 311–323.

Woinarski, J. C. Z., Brock, C., Fisher, A., Milne, D., & Oliver, B. (1999). Response of birds and reptiles to fire regimes on pastoral land in the Victoria River District, Northern Territory. *The Rangeland Journal, 21*, 24–38.

Woinarski, J. C. Z., Burbidge, A. A., & Harrison, P. L. (2015). Ongoing unraveling of a continental fauna: Decline and extinction of Australian mammals since European settlement. *Proceedings of the National Academy of Sciences of the United States of America, 112*, 4531–4540.

Woinarski, J. C. Z., & Legge, S. (2013). The impacts of fire on birds in Australia’s tropical savannas. *Emu – Austral Ornithology, 113*, 319–352.

Woinarski, J. C. Z., Legge, S., Fitzsimons, J. A., Traill, B. J., Burbidge, A. A., Fisher, A., … Ziebicki, M. (2011). The disappeared mammal fauna of northern Australia: Context, cause and response. *Conservation Letters, 4*, 192–201.

Woinarski, J. C. Z., Williams, R. J., Price, O., & Rankmore, B. (2005). Landscapes without boundaries: Wildlife and their environments in northern Australia. *Wildlife Research, 32*, 377–388.

Woinarski, J. C. Z., & Winderlich, S. (2014). A strategy for the conservation of threatened species and threatened ecological communities in Kakadu National Park 2014–2024. Darwin: North Australian Hub of the National Environmental Research Program.

Woolley, L. A., Murphy, B. P., Radford, I. J., Westaway, J., & Woinarski, J. C. Z. (2018). Cyclones, fire, and termites: The drivers of tree hollow abundance in northern Australia’s mesic tropical savanna. *Forest Ecology and Management, 419*, 146–159.

Yates, C. P., Edwards, A. C., & Russell-Smith, J. (2009). Big fires and their ecological impacts in Australian savannas: Size and frequency matters. *International Journal of Wildland Fire, 17*, 768–781.

Ziebicki, M. R., Woinarski, J. C. Z., Webb, J. K., Vanderduys, E., Tuft, K., Smith, J., … Burbidge, A. A. (2015). Stemming the tide: Progress towards resolving the causes of decline and implementing management responses for the disappearing mammal fauna of northern Australia. *Therya, 6*, 169–225.

**SUPPORTING INFORMATION**

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