

Northern brown bandicoot (*Isoodon macrourus*) and common brushtail possum (*Trichosurus vulpecula*) density on the Tiwi Islands: insights and implications

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Abstract. Despite the ongoing collapse of native mammal populations across northern Australia, the paucity of robust estimates of population density limits our capacity to identify and understand population change. Here we aimed to provide the first estimates of native mammal density on the Tiwi Islands – one of Australia’s largest remaining refuge areas for native mammals. We conducted intensive live-trapping at four sites that represent varying combinations of fire frequency, feral cat density and feral herbivore presence. We used spatially-explicit capture-recapture models to investigate the density of common brushtail possum (*Trichosurus vulpecula*) and northern brown bandicoot (*Isoodon macrourus*). Compared with mainland northern Australia, populations of common brushtail possum and northern brown bandicoot have remained relatively healthy on the Tiwi Islands. Common brushtail possum density was significantly higher on Bathurst Island (1.06 possum ha⁻¹) compared with Melville Island (0.32 possum ha⁻¹), whereas northern brown bandicoot density varied across all four sites (ranging from 0.04 to 0.34 bandicoot ha⁻¹). Unexpectedly, the very frequently burnt Ranku site (Bathurst Island) continues to support healthy populations of both species. These density estimates provide critical information for identifying and understanding future population change for two species that have suffered marked declines across the Australian monsoon tropics. Although the lack of replication limits our ability to draw conclusions regarding the ecological constraints of these mammal populations, our density observations align with a recent conceptual model postulating that the persistence of native mammal populations across northern Australian savannas reflects a complex, but spatially-variable interplay of ‘bottom-up’ and ‘top-down’ processes.

Keywords: Bathurst Island, capture-recapture, common brushtail possum, decline, habitat refuge, mammal extinction, Melville Island, monsoon tropics, native mammals, northern Australia, northern brown bandicoot, savannas, Tiwi Islands.

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Introduction

Australia has experienced an extraordinarily high rate of mammal extinction in recent centuries. Ten percent of Australia’s native terrestrial mammal species have become extinct since European colonisation in 1788 (Woinarski *et al.* 2015), and many more have disappeared from most of their former ranges. The most dramatic declines occurred in arid central Australia prior to the mid-20th century. Until recent decades it was assumed that the vast, uncleared savannas of monsoonal northern Australia would retain a healthy assemblage of native mammals. However, research conducted since the 1990s has demonstrated that northern Australia’s native mammals are experiencing a rapid and severe decline (Woinarski *et al.* 2011), which, if continue unabated, will lead to more extinctions (Geyle *et al.* 2018).

The drivers of the current decline of native mammals across northern Australia have proven difficult to identify. However, a conceptual model has emerged over the past decade, postulating that frequent fire and heavy grazing by feral herbivores have degraded habitat, disrupting both ‘bottom-up’ (e.g. resource availability) and ‘top-down’ (e.g. predation) processes, resulting in the widespread decline of native mammal populations (Stobo-Wilson *et al.* 2020a).

Robust estimates of population density increase our ability to understand population change and our capacity to mitigate population decline (Efford 2004), such as those currently occurring across northern Australia. Recently, advances in statistical modelling have improved our ability to accurately estimate population density. For example, spatially-explicit capture-recapture models

take into account both the distribution and movement of individuals in relation to detectors (e.g. traps or motion-activated cameras) to provide estimates of density that are unbiased by edge-effects and imperfect detection (Efford 2004). Despite their utility, spatially-explicit estimates of population density are rare for northern Australian mammals. This likely reflects, in part, the diminished ability to obtain sufficient data required for these analytical methods due to the catastrophic declines suffered by native mammals across northern Australian savannas that occurred prior to the development of these methods. However, it appears that such data can still be obtained from areas of northern Australia, such as Groote Eylandt (Heiniger *et al.* 2018, 2020), the Tiwi Islands and Cobourg Peninsula (Stobo-Wilson *et al.* 2020a).

The Tiwi Islands, in the Australian monsoon tropics, are one of the last remaining areas in Australia to support an intact native mammal assemblage (Murphy and Davies 2014; Davies *et al.* 2018). However, due to the presence of threatening processes that have been implicated in the decline of native mammals across northern Australia including feral herbivores and feral cats (Davies *et al.* 2017, 2020), and worrying signs of initial decline (Davies *et al.* 2018), native mammal populations on these islands may be at risk. Here, we aimed to provide (1) estimates of native mammal density on the Tiwi Islands; and (2) insight into the ecological constraints of native mammal density in tropical savannas.

Materials and methods

Study site

Our study was conducted on Melville (5786 km²) and Bathurst Island (2600 km²), Australia's second and fifth largest islands,

respectively. They are the two largest of the group of islands collectively known as the Tiwi Islands, located 20 km off the north coast of Australia's Northern Territory (Fig. 1). The main vegetation type of the Tiwi Islands is lowland savanna dominated by *Eucalyptus miniata*, *Eucalyptus tetradonta* and *Corymbia nesophila* with a predominantly grassy understorey. The islands experience a tropical monsoonal climate with a humid wet season (November–March) in which over 90% of the annual rainfall occurs, followed by a dry season (April–October). Fire frequency is very high but there is significant variation across the islands (Fig. 1). Feral cats (*Felis catus*) are present on both islands, but recent work suggests that the density of feral cats is lower on Bathurst Island than Melville Island (Davies *et al.* 2021). Feral herbivores (Asian water buffalo *Bubalus bubalis* and horse *Equus caballus*) are only present on Melville Island. Feral pigs (*Sus scrofa*) are widespread on Bathurst Island, but localised to the western half of Melville Island. Cane toads (*Rhinella marina*) are absent from both islands. Dingoes (*Canis dingo*) are widespread across both islands.

Data collection

We conducted intensive live-trapping at four sites across the Tiwi Islands: two on Bathurst Island (Cape Fourcroy and Ranku) and two on Melville Island (Pickertaramoor and Cache Point) (Fig. 1). At each site, we deployed a trapping grid consisting of 300 live-traps (30 rows of 10) spaced 20 m apart, covering an area of ~0.1 km². Each grid was live-trapped for four consecutive nights at two separate times (June and September) in the dry season of 2019, a total of 9600 live-trap nights. On each grid, we used 75 cage traps (66 × 23 × 26 cm) and 225 box-type 'Sherman' traps (30 × 10 × 8 cm) baited with a standard

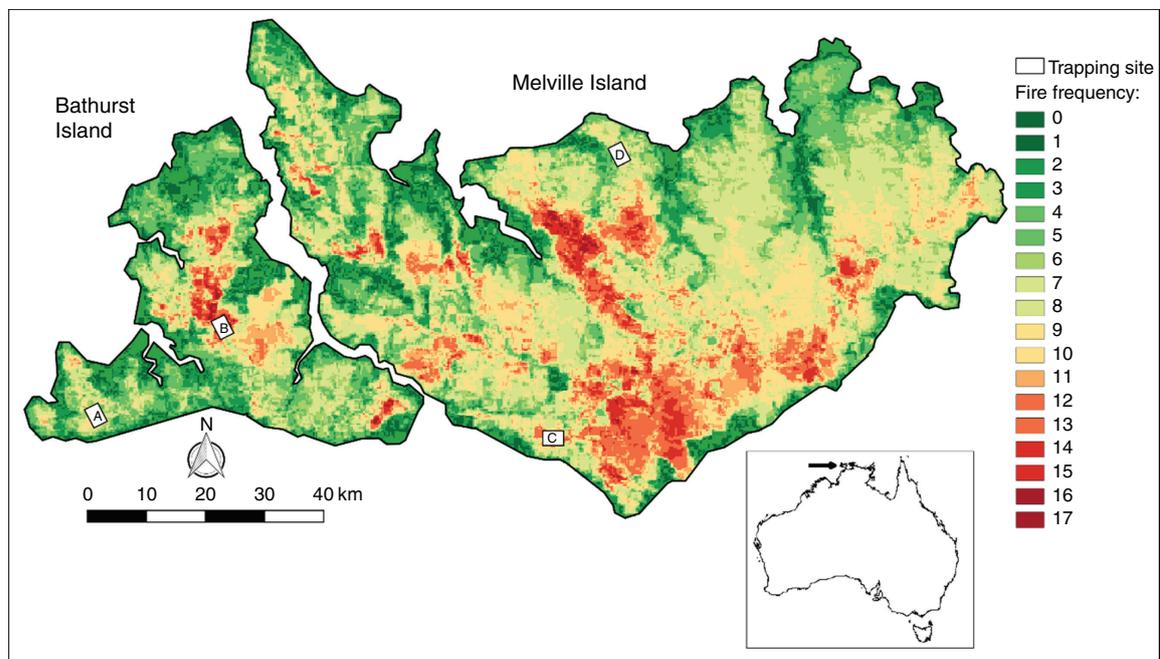


Fig. 1. Location of our four live-trapping sites on the Tiwi Islands (A – Cape Fourcroy; B – Ranku; C – Pickertaramoor; D – Cache Point). The background map indicates MODIS satellite-derived fire frequency (number of times burnt in the 17-year period 2000–2016, inclusive). The location of the Tiwi Islands relative to mainland Australia is also shown (inset).

Table 1. Summary of the sites and species capture counts

The number of individual animals is shown in the parentheses. Dashes indicate where grids were located outside the range of a particular species

	Cape Fourcroy	Ranku	Pickertaramoor	Cache Point	Total captures (individuals)
Island	Bathurst	Bathurst	Melville	Melville	
Fire frequency	Low	High	High	Low	
Feral herbivores present?	No	No	Yes	Yes	
Feral cat density	Low	Low	0.15 cats km ⁻²	0.15 cats km ⁻²	
Feral pigs present?	Yes	Yes	No	No	
Common brushtail possum (<i>Trichosurus vulpecula</i>)	81 (30)	77 (29)	28 (12)	16 (6)	202 (77)
Northern brown bandicoot (<i>Isodon macrourus</i>)	19 (7)	50 (18)	3 (2)	39 (17)	111 (44)
Delicate mouse (<i>Pseudomys delicatulus</i>)	0 (0)	14 (5)	1 (1)	10 (8)	25 (14)
Black-footed tree-rat (<i>Mesembriomys gouldii</i>)	–	–	8 (5)	8 (7)	16 (12)
Pale field-rat (<i>Rattus tunneyi</i>)	4 (1)	3 (2)	0 (0)	0 (0)	7 (3)
Butler's dunnart (<i>Sminthopsis butleri</i>)	1 (1)	0 (0)	0 (0)	1 (1)	2 (2)
Grassland melomys (<i>Melomys burtoni</i>)	0 (0)	0 (0)	0 (0)	1 (1)	1 (1)
Northern brush-tailed phascogale (<i>Phascogale pirata</i>)	0 (0)	0 (0)	0 (0)	1 (1)	1 (1)
Total captures (individuals)	105 (39)	144 (54)	40 (20)	76 (41)	365 (154)

mammal bait of oats, peanut butter and honey. Each captured animal was individually marked with a numbered ear tag (Style 1005-1; National Band and Tag Company, Newport, KY, USA) and a microchip (ID-100VB/1.4; Trovan Ltd, Cologne, Germany) implanted between the scapulae.

As we aimed to explore the environmental correlates of native mammal density across the Tiwi Islands, the locations of the four sites were chosen to represent varying combinations of fire frequency, feral cat density and feral herbivore presence (Table 1). The Pickertaramoor and Ranku sites were characterised by very high fire frequency, with the MODIS satellite-derived fire frequency recorded at each individual trap location, averaging 13.7 and 14.3 across each grid, respectively. The Cache Point and Cape Fourcroy sites were placed in areas with lower fire frequency, with the MODIS satellite-derived fire frequency recorded at each individual trap location, averaging 6.4 and 8.1 across each grid, respectively. Feral cat density was highest at Pickertaramoor and Cache Point, and exceptionally low at both the Ranku and Cape Fourcroy sites. Feral herbivores were present at both Pickertaramoor and Cache Point, and absent from Bathurst Island.

Data analysis

To investigate the variation in native mammal density across the four sites, we fitted spatially-explicit capture–recapture models using the ‘secr’ package (Efford 2020) in the statistical program R (R Development Core Team 2013). We collapsed the total number of trap nights conducted at each location (eight) into 24-h sampling occasions. We used a 500-m buffer around the outermost coordinates of the live-trapping grids to ensure that density was estimated over a large enough area to include all small native mammals exposed to our survey (Royle *et al.* 2013).

To investigate the variation of native mammal density across our four sites, we ran four multi-session models for each species: constant density across all sites (Density ~ 1), density predicted by site (Density ~ Site), density predicted by island (Density ~ Island) and density predicted by fire frequency (Density ~ Fire frequency). To account for seasonal variation in native mammal

detectability, we included a categorical variable (Survey) as a predictor of the two detection parameters: g_0 (the probability of detecting an animal (per occasion) if a trap was to be placed at its home-range centre) and σ (the reduction in detection probability with distance from a home-range centre). Model selection based on Akaike's information criterion adjusted for small sample size (AIC_c) was used to identify the best fit model (Burnham and Anderson 2002), from which estimates of native mammal density were obtained (Table 2).

Results

From 9600 live-trap nights, we recorded a total of 365 captures of 154 individual native mammals, from eight species (Table 1). Common brushtail possum and northern brown bandicoot were by far the most commonly trapped species, with 202 captures of 77 individual possums and 111 captures of 44 individual bandicoots (Table 1). However, there was considerable variation in the number of captures of each of these species between the four sites. For example, we recorded 81 captures of 30 individual possums at Cape Fourcroy but only 16 captures of 6 individuals at Cache Point. Similarly, captures of northern brown bandicoot varied from 50 at Ranku to just 3 at Pickertaramoor.

Capture rates were sufficient to investigate population density using spatially-explicit capture–recapture analyses for both the common brushtail possum and northern brown bandicoot. Variation in common brushtail possum density was best explained by island (Table 1), with the estimated possum density on Bathurst Island (1.06 ha⁻¹) significantly higher than on Melville Island (0.32 ha⁻¹) (Fig. 2). Variation in northern brown bandicoot density was best explained by site (Table 1), ranging from 0.04 ha⁻¹ at Pickertaramoor to 0.34 ha⁻¹ at Ranku (Fig. 3).

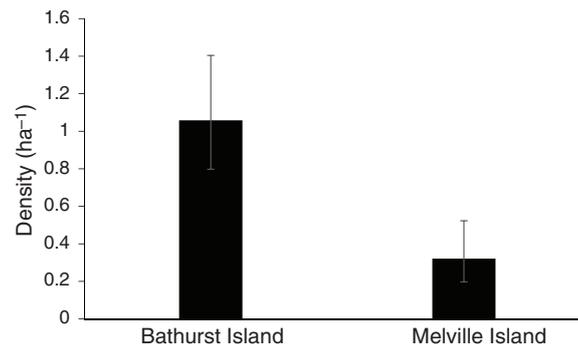
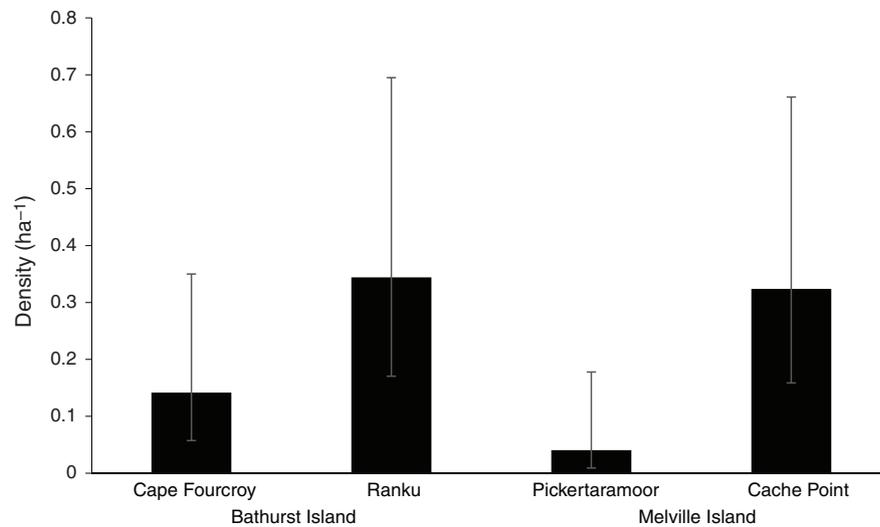
Discussion

We have provided the first robust population density estimates for common brushtail possum and northern brown bandicoot on

Table 2. Summary of the models investigating the density of common brushtail possum and northern brown bandicoot on the Tiwi Islands

k , number of parameters; AICc, Akaike's information criterion adjusted for small sample size; Δ AICc, difference between the AICc of this model and the model with the smallest AICc; w_i , Akaike weight. Survey = categorical variable to account for potential seasonal differences in the two detection parameters (g_0 and σ)

Model	k	Δ AICc	w_i
Common brushtail possum (<i>Trichosurus vulpecula</i>)			
Density ~ Island, g_0 ~ Survey, σ ~ Survey	6	0.0	0.85
Density ~ Site, g_0 ~ Survey, σ ~ Survey	8	3.4	0.15
Density ~ 1, g_0 ~ Survey, σ ~ Survey	5	19.5	0.00
Density ~ Fire frequency, g_0 ~ Survey, σ ~ Survey	6	21.8	0.00
Northern brown bandicoot (<i>Isoodon macrourus</i>)			
Density ~ Site, g_0 ~ Survey, σ ~ Survey	8	0.0	0.99
Density ~ 1, g_0 ~ Survey, σ ~ Survey	5	8.8	0.01
Density ~ Island, g_0 ~ Survey, σ ~ Survey	6	10.7	0.00
Density ~ Fire frequency, g_0 ~ Survey, σ ~ Survey	6	11.2	0.00

**Fig. 2.** Mean density of common brushtail possum on Melville and Bathurst Island. Error bars indicate 95% confidence intervals.**Fig. 3.** Mean density of northern brown bandicoot at each of the four sites across the Tiwi Islands. Error bars indicate 95% confidence intervals.

the Tiwi Islands, one of the last remaining areas in Australia to retain a complete assemblage of native mammals (Burbidge *et al.* 2009). Our density estimates support the view that populations of these species on the Tiwi Islands have remained relatively healthy compared with adjacent parts of the mainland. Albeit from only four locations, we have provided critical information for identifying and understanding future population change for two species that have suffered marked declines across the Australian monsoon tropics. Although the lack of replication limits our ability to draw conclusions regarding the ecological constraints of these mammal populations, our observations provide valuable insight, and align with a recent conceptual model postulating that the persistence of native mammal populations across northern Australian savannas reflects a complex, but spatially-variable interplay of 'bottom-up' (e.g. resource availability) and 'top-down' (e.g. predation) processes.

Unfortunately, there are very few recent density estimates for the common brushtail possum or northern brown bandicoot that are directly comparable to our results. Kerle (1998) analysed survey data collected between 1979 and 1981 in an area of lowland woodland in Kakadu National Park and estimated the population density of common brushtail possum to be 3.1 ha^{-1} , roughly three times higher than our estimate of possum density on Bathurst Island (1.06 ha^{-1}). A decade later, using data collected as part of a large-scale fire experiment between 1990 and 1994 (Andersen *et al.* 1998), Griffiths (2013) estimated the density of possums and bandicoots across the Kapalga area of Kakadu National Park to be 0.78 and 0.79 ha^{-1} , respectively. Pope (2001) estimated northern brown bandicoot density to range from 0.073 to 0.103 ha^{-1} in an area of dry eucalypt forest in the wet tropics of northern Queensland. The most directly comparable estimate of northern brown bandicoot population density comes from another island refuge off the northern Australian coast – Groote Eylandt (Heiniger *et al.* 2018). Using spatially-explicit capture-recapture models, Heiniger *et al.* (2018) estimated northern brown bandicoot population density to be 0.19 ha^{-1} (95% CI 0.13–0.36).

As common brushtail possum density on Bathurst Island (1.06 ha^{-1}) remains higher than that recorded prior to widespread mammal decline in Kakadu (0.78 ha^{-1}) (Griffiths 2013), our results concur with Firth *et al.* (2006), who concluded that possum populations on Bathurst Island have remained healthy compared with areas of mainland northern Australia. Although possum density on Melville Island (0.32 ha^{-1}) is significantly lower than on Bathurst Island, a recent island-wide survey of historical sites on Melville Island demonstrated that possums are widespread, and found no significant decrease in possum trap-success since 2000, suggesting possum populations on Melville Island also remain healthy compared with areas on the mainland (Davies *et al.* 2018). Davies *et al.* (2018) found that while northern brown bandicoot trap-success on Melville Island decreased by 90% between 2000 and 2015, this species also remains widespread. Here, we have demonstrated that in some areas of the Tiwi Islands, northern brown bandicoot populations remain in relatively high densities, such as at Ranku (0.34 ha^{-1}) and Cache Point (0.32 ha^{-1}). However, only two individual bandicoots were recorded at the Pickertaramoor grid, with density estimated at a low 0.04 ha^{-1} .

Given the paucity of robust and consistent estimates of population density, indices of relative abundance (i.e. trap-success) have more commonly been used to identify, and investigate the decline of native mammal species across northern Australian savannas (Woinarski *et al.* 2001, 2010). However, the validity of using indices of relative abundance as an accurate measure of population size has been questioned (Slade and Blair 2000), especially when imperfect detection is ignored (MacKenzie and Kendall 2002). Unfortunately, as the data required for spatially-explicit estimates of population density can be demanding to collect, there is often a trade-off with how many replicate sites can be surveyed. Our density estimates provide critical information for identifying and understanding future population change for two species that have suffered marked decline across the Australian monsoon tropics. Our density estimates also represent the robust information on population size that can ensure the accurate listing of species on the IUCN's Red List of Threatened Species (IUCN 1996).

Patterns of native mammal persistence/decline across northern Australian savannas reflect a complex interplay of 'bottom-up' and 'top-down' processes (Stobo-Wilson *et al.* 2020a). As such, the variation in the density of common brushtail possum and northern brown bandicoot demonstrated here likely reflects multiple contributing factors. The high density of possums on Bathurst Island might reflect the greater availability of den sites (i.e. tree hollows) often associated with the dense, and well-developed eucalypt forests that occur on Bathurst Island (compared with Melville Island) (Woolley *et al.* 2018). The absence of the black-footed tree-rat (*Mesembriomys gouldii*) from Bathurst Island may also help explain the higher density of possums, due to less intraspecific competition for den sites compared with Melville Island (Pittman 2003; Firth *et al.* 2006). The higher density of possums on Bathurst Island may also reflect a higher availability of important food and shelter resources due to the absence of Asian water buffalo (*Bubalus bubalis*) and horse (*Equus caballus*), both of which are present on Melville Island (Stobo-Wilson *et al.* 2020a). The predation pressure on native mammal populations on Bathurst Island is also likely to be lower than on Melville Island due to the low density of feral cats (Davies *et al.* 2021).

Despite the very high frequency of fire at the Ranku site, populations of common brushtail possum and northern brown bandicoot in this area remain healthy. This was an unexpected result because frequent fire is often thought to make environmental conditions unfavourable for these species, due to the removal of critical food and shelter resources (Kerle 1998; Pardon *et al.* 2003; Griffiths and Brook 2015) and heightened exposure to predation (Stobo-Wilson *et al.* 2020b). It may be that in this area the negative impacts associated with very frequent fire are outweighed by the benefits associated with high productivity, the absence of feral herbivores and possibly lower predation pressure, thereby allowing populations to remain healthy. The Pickertaramoor site provides an interesting comparison to Ranku. Despite being similarly frequently burnt to the Ranku site, we recorded by far the lowest overall number of native mammal captures and individuals, and estimated a very low density of northern brown bandicoot (0.04 ha^{-1}) at Pickertaramoor. Among our four sites, Pickertaramoor is characterised as the most degraded, with the highest activity of

predators (feral cats and dingoes) and feral herbivores (Davies *et al.* 2021). In this area (contrary to the situation at Ranku), the negative impacts of very frequent fire are likely exacerbated by habitat degradation by feral herbivores and higher predation pressure, reducing the capacity of native mammal populations to persist.

Our results suggest that in productive northern Australian savannas, frequent fire may not necessarily drive species decline when other threats are either absent or relatively mild. However, it is important to note that we have only investigated fire frequency, not intensity. As northern brown bandicoot have been shown to prefer sites that have experienced fine-scale low intensity fires (compared with both unburnt and extensively burnt sites) (Pardon *et al.* 2003; Firth *et al.* 2006), the variation in bandicoot density across our sites could reflect variation in fire intensity. Given that large, high-intensity fires are likely to be particularly detrimental to small mammals (Firth *et al.* 2010; Lawes *et al.* 2015), we suggest that future research uses metrics that go beyond fire frequency and better gauge actual fire impact.

Another important caveat of our study is that it was conducted at only four locations. Hence, our capacity for robust inference of the ecological constraints on native mammal density is limited. Increasing the spatiotemporal replication of robust estimates of population density (for a greater number of species), will lead to a better understanding of population trajectories under varying combinations of threatening processes, as well as a better capacity to gauge the effectiveness of management interventions. However, our results clearly align with a recent conceptual model postulating that the state of native mammal populations across northern Australian savannas reflects a complex, and spatially-variable interplay of ‘bottom-up’ (e.g. resource availability) and ‘top-down’ processes (e.g. predation) (Stobo-Wilson *et al.* 2020a). This has important management implications. For example, as possum and bandicoot populations remain healthy at the frequently burnt Ranku site, targeted fire management aimed at reducing fire frequency in this area may be unnecessary and not offer the same benefits to these species as if it were applied in other areas, such as Pickertaramoor. In other words, the benefits of targeted management actions can vary across the landscape depending on how the occurrence and severity of disturbance processes are mitigated by landscape productivity. Given limited operational budgets for management agencies, a more spatially-tailored approach to management, based on a greater understanding of how the occurrence and severity of disturbance processes are mitigated by landscape productivity, may be more effective.

Data availability

The data used in this publication are owned by the Tiwi Land Council. Access to this data can be negotiated with the Tiwi Land Council.

Conflicts of interest

The authors declare no conflicts of interest.

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