

Habitat structure facilitates coexistence of native and invasive mesopredators in an Australian tropical savanna

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ABSTRACT

Context. The introduction of the cat (*Felis catus*) to Australia has been a key driver of the decline and extinction of the continent's endemic mammals. Currently, there is no clear long-term solution to controlling feral populations of cats at a landscape scale. As such, understanding how environmental conditions and habitat attributes can mediate the coexistence between introduced predators and native mammals can improve management outcomes for threatened species. **Aim.** We sought to compare the differences in habitat use by feral cats and a remnant population of the endangered northern quoll (*Dasyurus hallucatus*) to understand what environmental variables allow these two mesopredators to coexist in tropical savanna of Cape York Peninsula, Queensland. **Methods.** We deployed grids of motion-activated cameras three times per year over a 3-year period, across *Eucalyptus tetrodonta*-dominated plateaux known to be inhabited by feral cats and northern quolls. We modelled the spatial variation in the frequencies of detection of feral cats and northern quolls (referred to as 'habitat use'), as a function of biotic and abiotic environmental variables by using a generalised linear model for consistent variables and a generalised linear mixed-effect model for fluctuating variables. **Key results.** Habitat use by feral cats was most frequent in areas with high fire frequencies and low tree basal area, whereas habitat use by northern quolls was most frequent in areas of high basal area of *E. tetrodonta* (a commonly used den tree species), topographic ruggedness, and long-unburnt savanna. **Conclusions.** Frequent fires in tropical savanna promote habitat use by feral cats and can result in a reduction of critical habitat for northern quolls. **Implications.** We postulate that remnant populations of northern quolls on Cape York Peninsula occur in less frequently burnt refugia, primarily on top of plateaux that support high-biomass tropical savanna dominated by *E. tetrodonta*. Our findings highlighted that threatened mammals can persist alongside introduced predators in tropical savanna but are dependent on the maintenance of structurally complex habitat.

Keywords: conservation, ecology, environment, habitat use, introduced species, invasive species, predator–prey interactions, threatened species, wildlife management.

Introduction

Invasive predators are a serious threat to biodiversity globally (Blackburn *et al.* 2004; Doherty *et al.* 2016; Dueñas *et al.* 2021). Some of the most important ways predators can affect ecological communities are by killing prey species and suppressing and/or excluding sympatric predators (Tannerfeldt *et al.* 2002; Cáceres *et al.* 2009). These impacts can be strongly accentuated when native species exhibit naivety towards invasive predators, typically through a lack of shared evolutionary history (Sih *et al.* 2010). As a result, 142 terrestrial species have become extinct through the impacts of invasive mammalian predators, with a further ~600 species still being threatened globally (Doherty *et al.* 2016).

Many invasive mammal species have benefited from human-assisted migration and are now firmly established across the globe (Long 2003; Clout *et al.* 2008). The introduction of

the cat (*Felis catus*) to Australia by Europeans in the late 18th Century has had a catastrophic impact on native wildlife (Abbott 2008; Doherty *et al.* 2017). Taking advantage of naïve native prey, the proliferation of introduced prey species, and the paucity of large, native predators, cats quickly dispersed across the continent, with feral populations becoming established in all of Australia's bioregions (Abbott 2008; Doherty *et al.* 2014; Legge *et al.* 2020). The extinction of at least 26 of Australia's native mammal species has been associated with cat predation, with a further ~75 native mammal species being currently threatened (Woinarski *et al.* 2019). Invasive predators, such as the cat, are still a significant threat to many native mammal species, posing an urgent need to curtail their impact on threatened species.

Efforts to control feral cat populations are often limited by scale, effort, and cost (Campbell *et al.* 2011; Parkes *et al.* 2014; Baker and Bode 2016). Complete eradication of invasive predators is seen as the most beneficial, long-term solution to conserving threatened fauna (Jones *et al.* 2016; Holmes *et al.* 2019), but to do so often requires extensive monitoring to ensure success, can be cost prohibitive at large scale and, even when conducted using best practices, can have negative, unintended outcomes (Bodey *et al.* 2011; Lazenby *et al.* 2014; Holmes *et al.* 2019). Successful eradications have occurred on off-shore islands up to 630 km² in area (Campbell *et al.* 2011) and in increasingly large, predator-free fenced reserves (Legge *et al.* 2018). However, open landscape-scale control programs are often hampered by the continual immigration of cats into areas with cat control (Doherty *et al.* 2017). These challenges mean eradication may not always be a viable or appropriate solution to conserving native wildlife threatened by invasive species.

Instead of eradication, manipulation of ecological factors that limit feral cat populations may be a more feasible and cost-effective approach to control cats (Doherty *et al.* 2015; Miritis *et al.* 2020). For example, research suggests that in northern Australia's savanna landscapes cats have a strong association with frequently burnt habitat and open, heavily grazed areas, because the reduced vegetation cover in both cases may improve hunting success (McGregor *et al.* 2014, 2015; Davies *et al.* 2020). Australia's only mammalian apex predator, the dingo (*Canis familiaris*), has been found to consume cats (Doherty *et al.* 2019), suggesting a degree of top-down predation pressure on feral cat activity. Although, the role dingoes play in suppressing cat activity is heavily debated (Letnic *et al.* 2012; Fancourt *et al.* 2019; Kreplins *et al.* 2021), with experimental removal of dingoes not having been found to increase feral cat abundances in response (Letnic *et al.* 2009; Castle *et al.* 2021). As such, this poses a need to identify how environmental factors limit cat activity and what potential landscape solutions can reduce the impact cat predation has on threatened mammals.

In this study, we investigated the spatial patterns of habitat use by cats and a coexisting native mesopredator, the northern

quoll (*Dasyurus hallucatus*), in tropical savanna at Weipa on Cape York Peninsula, Queensland. The northern quoll is the largest native mammalian mesopredator across northern Australia, and the smallest member of the genus *Dasyurus*, weighing between ~400 and 1200 g (Van Dyck and Strahan 2008). The current distribution of the northern quoll extends patchily across monsoonal northern Australia (Moore *et al.* 2022; Fig. 1). Despite the northern quoll's widespread distribution, it has suffered significant population declines in recent decades (Braithwaite and Griffiths 1994; Moore *et al.* 2019), and is considered *Endangered* (Oakwood *et al.* 2016). One of the major drivers of the decline of the northern quoll, especially in higher-rainfall regions, is poisoning following ingestion of the toxic and invasive cane toad (*Rhinella marina*; Covacevich and Archer 1975; Burnett 1997). However, other drivers of the decline of the northern quoll are thought to include predation by feral cats, high fire frequencies and habitat degradation by introduced herbivores (Braithwaite and Griffiths 1994; Moore *et al.* 2022). Lowland savanna populations of northern quolls seem to be the most severely affected by these threats, whereas high-rainfall regions and topographically rugged habitat harbour the largest remnant populations (Braithwaite and Griffiths 1994; Oakwood 2000; Moore *et al.* 2019). Despite these observed trends, our study population of northern quolls has been found to reside in tropical savanna that lacks extensive topographical ruggedness and is inhabited by both cats and cane toads. As such, this remnant northern quoll population provides an excellent model system to understand how environmental conditions and habitat attributes can contribute to the persistence of native mammals alongside cats and will assist in developing appropriate strategies for managing habitat that facilitates coexistence.

To infer how cats and northern quolls can coexist within tropical savanna, we aimed to identify the environmental variables that were the strongest drivers of cat and northern quoll habitat use. We investigated a range of ground-based and satellite-derived variables that have been previously identified as influencing spatial patterns of cats and native small mammals across the northern Australia, including fire regimes (Woinarski *et al.* 2010; Griffiths *et al.* 2015; McGregor *et al.* 2016; Davies *et al.* 2020), vegetation structure (Hernandez-Santin *et al.* 2016; Stobo-Wilson *et al.* 2020a, 2020b), water proximity (McGregor *et al.* 2016; Moore *et al.* 2019) and topographical attributes (Hernandez-Santin *et al.* 2016; Moore *et al.* 2019; McDonald *et al.* 2020). On the basis of these previous findings and the conditions of the plateau environment, we predicted that the environmental conditions and attributes found atop the plateaux would be most frequently used by northern quolls, whereas the environmental conditions and attributes found in low-lying savannas surrounding the plateaux would be most frequently used by cats.

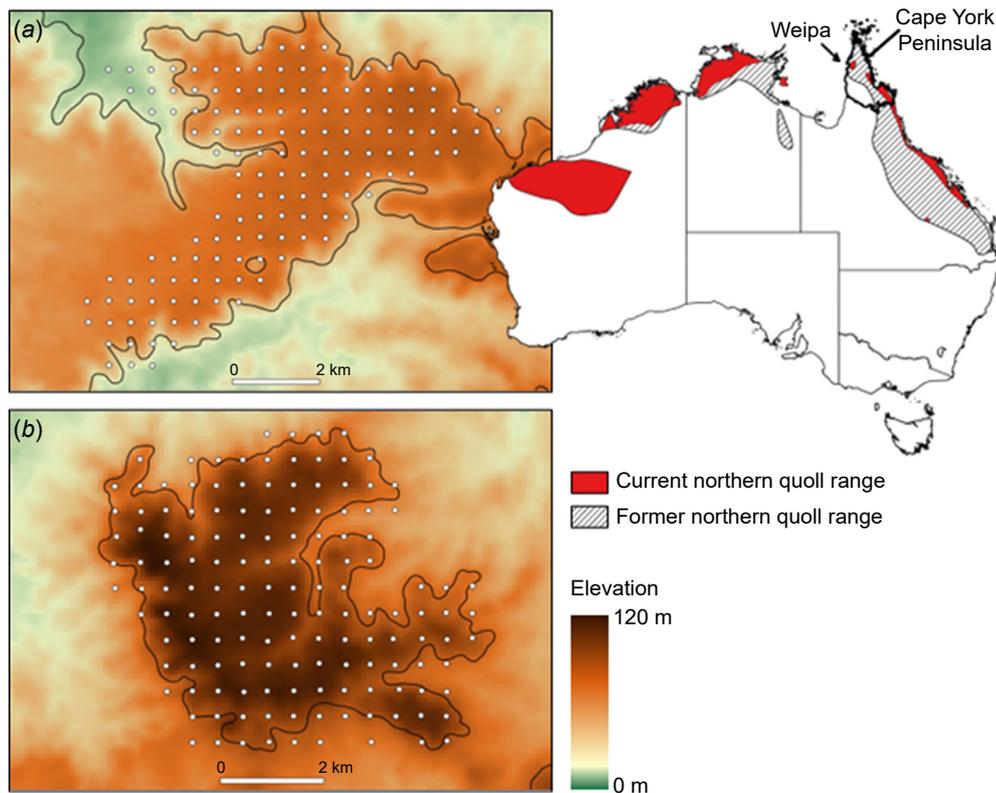


Fig. 1. Camera-trap grids across (a) the northern plateau and (b) the southern plateau with respect to elevation near Weipa on the Cape York Peninsula, Queensland. White circles represent individual camera-trap sites. Black lines represent the plateau vegetation community. The inset map shows the current and former range of the northern quoll (Moore et al. 2022).

Materials and methods

Study species

The northern quoll is a highly adaptable, generalist mesopredator that occurs in a variety of habitats, including tropical savanna, monsoon rainforest, and rocky outcrops (Moore et al. 2022). As a generalist omnivore, the northern quoll consumes a varied diet consisting of fruits, seeds, and live prey such as rodents, reptiles and invertebrates (Dunlop et al. 2017). It also uses a wide variety of denning resources such as tree hollows, fallen logs, rock crevices and termite mounds, depending on the availability of hollow resources in the landscape (Oakwood 1997).

The northern quoll was once common across Cape York Peninsula (Fig. 1), inhabiting both the savannas of the western coast and the rainforests of the eastern coast (Braithwaite and Griffiths 1994). It is believed that the spread of the cane toad throughout Cape York Peninsula by the 1980s resulted in a widespread extirpation of northern quoll populations (Burnett 1997). The cane toad was first introduced to Australia in 1935, to control the native cane beetle (*Dermolepida albobirtum*); however, the cane toad also secretes potent poisons, collectively termed bufotoxin,

that is lethal on ingestion by the northern quoll (Ujvari et al. 2013). Despite this prominent threat, the northern quoll was observed to be in decline prior to cane toad arrival and is currently in decline in regions where the cane toad is yet to colonise, such as in the Pilbara region of Western Australia (Braithwaite and Griffiths 1994; Woinarski et al. 2011; Moore et al. 2022). The remnant population of northern quolls on which our study focuses was discovered in 2013, on bauxite plateaux near the town of Weipa (Fig. 1). Prior to that, the northern quoll had not been recorded in the Weipa region since 1985 (Winter and Atherton 1985). The area of occupancy and number of northern quoll populations elsewhere across Cape York Peninsula are not known.

Study area

The study area is located on the north-western coast of Cape York Peninsula in north-eastern Australia, east of the town of Weipa. The region has a tropical monsoonal climate, with 90% of the mean annual rainfall of 1700 mm typically falling in the summer wet season (December–April; Australian Bureau of Meteorology 2021). The landscape is characterised by elevated bauxite plateaux, dominated by tall, dense

savanna, interspersed between low-lying plains, dominated by open savanna, and river tributaries. The bauxite plateaux absorb large quantities of water during the wet season, which gets slowly released through springheads during the dry season, flowing down channels into the surrounding landscape (Specht *et al.* 1977; Leblanc *et al.* 2015). This hydrology allows for the formation of tall savannas with high tree biomass and a dense understorey (Bowman and Fensham 1991).

The study was undertaken across two bauxite plateaux known to be inhabited by both cats and northern quolls. Each plateau is approximately 45 km² in area, with elevations of 20 m and 100 m respectively, above the surrounding low-lying, open savanna. The vegetation of both plateaux consists of a sparse canopy dominated by *Eucalyptus tetrodonta* 25–35 m in height, with subdominant trees *Corymbia nesophila*, *C. stockeri* and *Erythrophleum chlorostachys*. Fruit-bearing trees such as *Pandanus spiralis*, *Livistona muelleri*, *Parinari nonda*, *Xylomelum scottianum* and *Planchonia careya* dominate the mid-storey, and the ground layer is dominated by annual and perennial grasses such as *Sarga plumosum*, *Heteropogon triticeus*, *Alloteropsis semialata* and *Eulalia mackinlayi*. Large termite mounds and hollow trees, both of which are known to be used for denning by the northern quoll, are common. Each plateau has some rugged, pronounced edges, but most of the plateau boundaries are gentle inclines with extensive ecotonal areas of intergrading vegetation communities. Neither plateau, nor the surrounding habitat, has significant areas of exposed rock.

The plateaux are characterised by reduced fire frequencies compared with the surrounding low-lying savanna (~0.6 fires year⁻¹ for plateaux vs 0.9 fires year⁻¹ for the surrounding low-lying savanna over a 20-year period; North Australian Fire Information 2021). Hazard-reduction burns are undertaken at the northern plateau (Fig. 1a) during the early dry season (May–July), but no such burns occur on the southern plateau (Fig. 1b). High-intensity wildfires occasionally occur, typically in the late dry season (August–November).

Camera surveys

Camera grids, targeting northern quolls, were established across both plateaux and immediately adjacent areas in 2018, and surveyed annually to 2020 (i.e. 2018, 2019 and 2020). Each camera grid consisted of 143 motion-activated cameras (PC800 Hyperfire Professional IR; Reconyx Inc., Holmen, WI, USA) at a grid spacing of 500 m × 500 m (Fig. 1). Each camera was attached to a tree with a bracket 1.5 m above the ground. Each camera faced straight down at a bait tube containing dried chicken meat. Cameras were active continuously (i.e. 24 h each day), and programmed to capture three images per trigger, with a high sensitivity. Cameras were deployed for a minimum of 10 nights in April–May of each year, to coincide with the northern quoll

breeding season, when individuals are most numerous and active. All 143 cameras deployed within each plateau grid were operated simultaneously. Between plateau grids, there were slight differences in camera operation times due to the time restraints of deployment. In total, 12 599 trap nights were sampled over 3 years, from 286 camera sites across the two plateaux.

Camera grids, targeting cats, were established across the northern plateau and immediately adjacent areas in 2018 and then both the north and south plateaux in 2019. No targeted cat surveys were undertaken in 2020. All cameras deployed within the cat grids were located at a subset of northern quoll grid camera locations. Each grid consisted of 70 cameras, a mix of HC600 Hyperfire Full Covert IR (Reconyx Inc.) and PC800 Hyperfire Professional IR (Reconyx Inc.), at a grid spacing of 500 m × 500 m. Each camera was attached to a tree at a height of 50 cm above the ground. Each camera was pointed towards the same point as the baited (northern quoll) cameras, approximately 2 m away, at an angle of approximately 20° below horizontal. Even though these cameras were not specifically baited to attract cats, deployments often occurred simultaneously with the baited-camera surveys targeting northern quolls or had residual scents from prior baiting surveys. Previous research has not shown an effect of food odours in promoting feral cat visitation (Read *et al.* 2015; Stokeld *et al.* 2015), with dried meat being a less receptive bait option for feral cats (Risbey *et al.* 1997; Moseby *et al.* 2011). With this consideration, we consider it unlikely that this overlap in bait deployment had a significant impact on our detection frequency of cats. Cameras were deployed for a minimum of 30 days in April–May and October–November of each year. All 70 cameras deployed within each plateau grid were operated simultaneously. Between plateau grids, there were slight differences in camera operation times owing to the time restraints of deployment. They were programmed to take three image bursts per trigger with high sensitivity and 24-h activity. In total, 15 228 trap nights were sampled over 2 years from 140 camera sites across the two plateaux.

The placement of each camera grid was targeted atop the plateaux to prioritise surveying habitat that was inhabited by both species. We aimed to maximise our detections of both species across the plateaux to ensure a thorough analysis of each species' use of the habitat conditions present. Permission for animal use was authorised by the Charles Darwin University Animal Ethics Committee (A18017) and the Queensland Department of Environment and Science (Scientific Purposes Permit WA0009373).

Environmental variables

We conducted ground-based vegetation surveys at each camera-trap site across the two plateaux in April–May 2019. We measured the basal area of all living and dead

trees with a diameter greater than 15 cm by using a basal-area sweep with a rod relascope (Wenger 1984; Oakwood 1997). Three sweeps were conducted along a 100-m transect to calculate the tree basal area ($\text{m}^2 \text{ha}^{-1}$) of the stand at each camera site. From this dataset, we calculated the total tree basal area and the basal area of *E. tetradonta*, given that *E. tetradonta* is the species most frequently used as a den tree by the northern quoll (G. J. Trewella, unpubl. data) for each camera-trap site.

We also derived several variables from satellite products. To measure the productivity and extent of vegetation, we calculated an average normalised-difference vegetation index (NDVI) for each camera-trap site by using 3 years (2018–2020) of Sentinel-2 satellite imagery collected from the months of June and July (European Space Agency 2021), so as to produce an average value for each site. To quantify the fire regimes of the region, we calculated an average annual fire frequency (fire years⁻¹) and time since last fire (days) at each camera-trap site by using 4 years of high-resolution (20 m) Sentinel-2 satellite imagery (European Space Agency 2021) from all useable images since the inception of Sentinel-2 in 2015. To measure the prominent topographical attributes of the landscape, we calculated elevation and a topographic ruggedness index (TRI; Riley et al. 1999) from a three arc-second digital elevation model (Department of Natural Resources, Mines and Energy 2018a) for each camera-trap site. We also calculated the distance to the nearest water source from surface hydrology line maps (Crossman and Li 2015) and the distance of each camera site to the plateau edge, using a vegetation map (scale: 1:100 000; Department of Natural Resources, Mines and Energy 2018b). In the case of distance to plateau edge, if the camera site was on the plateau, it was given a positive value, and if the camera site was off the plateau, it was given a negative value; hence, the variable ‘distance to plateau edge’ ranged from large negative values (far off the plateau) to large positive values (close to the centre of the plateau).

Statistical analysis

All statistical analysis was undertaken in R, ver. 3.6.3 (R Core Team 2020). We analysed two response variables, namely, the frequency of habitat use by (1) cats, and (2) northern quolls. The frequency of habitat use was expressed as the proportion of nights (i.e. 24-h periods, from midday to midday) in which the target species was detected.

Two modelling approaches were used to assess the extent to which frequency of habitat use by cats and northern quolls was correlated with environmental variables. Generalised linear modelling (GLM) was used to analyse the frequency of habitat use across all camera sites, by using all environmental variables apart from time-since-fire. Generalised linear mixed-effects modelling (GLMM) was used to analyse frequency of habitat use across all camera sites by using

only time-since-fire, with camera site being included as a random effect. Both the GLMs and GLMMs used a binomial error family, given that the response variable was a proportion (i.e. a two-column variable of nights the target species was detected and not detected). All continuous variables were centred and standardised prior to analysis, and we confirmed that there was not excessive collinearity ($r \leq 0.7$) among environmental variables (Zuur et al. 2010).

Generalised linear modelling

For each species, the 3 years of cat and northern quoll camera-survey detection histories were pooled to create a sole nightly detection/non-detection response variable at each camera-trap site. Because of the differences in camera-survey methods, a nuisance variable termed ‘camera index’, derived from the percentage of cat survey (forward-facing cameras) nights against the total survey nights (forward-facing camera nights and downward-facing camera nights), was included to account for differences in detection probability of each camera-survey method. On the basis of previous unpublished surveys in the region, our understanding is that northern quolls are largely restricted to the bauxite plateaux, whereas cats have been found to move throughout the landscape. As such, we selected slightly different variables to analyse for each species. To model the spatial variation in frequency of cat habitat use, we selected a global model that included the following variables: fire frequency, total basal area, elevation, distance to plateau edge, NDVI, distance to water, topographical ruggedness index and camera index. To model the spatial variation in frequency of northern quoll habitat use, we selected a global model that included the following variables: fire frequency, total basal area, *E. tetradonta* basal area, distance to plateau edge, NDVI, distance to water, topographical ruggedness index and camera index. We chose to include elevation as a variable for cat habitat use, to identify whether there was a general preference for elevated habitat (plateau) or low-lying habitat, owing to the observed transient behaviour of cats around the plateaux. We also chose to include the basal area of *E. tetradonta* as a variable for northern quoll habitat use because this tree species is a primary den tree for northern quoll in the Weipa region (G. J. Trewella, unpubl. data) and, therefore, a significant environment resource.

The global GLM models of frequency of habitat use by each species were produced using the R package ‘stats’ (R Core Team 2020) and all 128 possible models for each species were evaluated using the R package ‘MuMIn’ (Bartoń 2020). Significant overdispersion was present in the global models; so, QAICc (quasi-likelihood-corrected Akaike’s information criterion) was used to rank models (Burnham and Anderson 1998). To account for the overdispersion, each model was converted to a quasibinomial error structure to estimate model parameters, their standard errors and 95% confidence intervals. Following the information-theoretic

approach, all models were averaged to produce conditional parameter estimations (Burnham and Anderson 1998). The sum of Akaike weights for each variable was calculated to indicate relative importance (Symonds and Moussalli 2011).

Generalised linear mixed-effects modelling

For each species, the detection history of each camera-trap site per survey over the 3-year study period was recorded as a nightly detection/non-detection response variable. Time-since-fire was calculated from the starting date of each survey at each camera-trap site. If a fire occurred during a survey period, then an additional datapoint was included for that camera-trap site with a time-since-fire value of 1 day. For each species, three models were constructed using the R package 'glmmTMB' (Brooks *et al.* 2017), namely, a null model with a binomial error structure, a single variable (time-since-fire) model with a binomial error structure and a single-variable (time-since-fire) model with a beta-binomial error structure to account for overdispersion. All models included camera site as a random effect. The best fitting model for each species was selected for using the lowest AICc (corrected Akaike's information criteria).

Results

Frequency of habitat use by cats

In total, 274 cat detections were recorded across 27 827 trap nights over the 3-year period. Detections occurred at least once at 135 of 286 camera sites (47%). The mean annual naïve occupancy (i.e. the proportion of sites where cats were recorded) of the northern plateau was 24%. The mean annual naïve occupancy of the southern plateau was 19%.

The frequency of habitat use by cats was clearly correlated with two environmental variables, namely, fire frequency and tree basal area (Fig. 2). These were the only variables present in all well supported models ($\Delta\text{QAICc} \leq 2$; Table 1). Fire frequency had a clear, positive relationship with habitat use by cats; at the least frequently burnt sites (0.25 fires year⁻¹, i.e. one fire every 4 years), cats were very unlikely to be detected (proportion of nights with detection at <0.01 [CI: 0.003–0.007]); at the most frequently burnt sites (1.5 fires year⁻¹, i.e. three fires every 2 years), cats were much more likely to be detected (proportion of nights with detections at 0.04 [CI: 0.02–0.08]; Fig. 3a). Tree basal area had a clear negative relationship with habitat use; at sites with the highest basal area (40 m² ha⁻¹), cats were very unlikely to be detected (proportion of nights with detections at <0.01 [CI: 0.002–0.009]); at sites with the lowest basal area (10 m² ha⁻¹), cats were modestly more likely to be detected (proportion of nights with detections at 0.02 [CI: 0.01–0.02]; Fig. 3b).

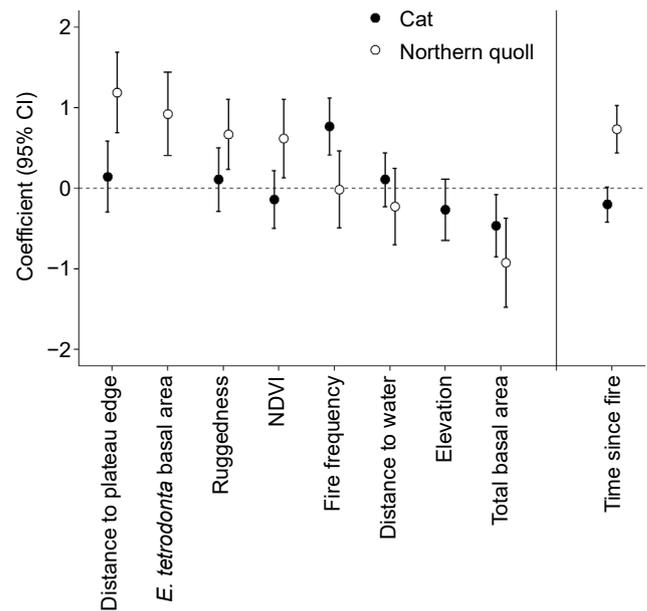


Fig. 2. Conditional regression coefficients of all predictor variables for cat and northern quoll habitat use derived from generalised linear modelling are shown on the left of the solid vertical line, and beta coefficients of time-since-fire for cat and northern quoll habitat use derived from generalised linear mixed effect modelling are shown on the right. Error bars represent the 95% confidence intervals of each estimated coefficient. The dotted horizontal line represents a regression coefficient value of 0.

Frequency of habitat use by northern quolls

In total, 615 northern quoll detections were recorded across 27 827 trap nights over the 3-year period. Detections occurred at least once at 139 of 286 camera sites surveyed (49%). The average annual naïve occupancy of the northern plateau was 11%. The average annual naïve occupancy of the southern plateau was 38%.

The frequency of habitat use by northern quolls was clearly correlated with five environmental variables, namely, *E. tetradonta* basal area, total tree basal area, distance to plateau edge, topographic ruggedness index and NDVI (Fig. 2). These were the variables present in all well supported models ($\Delta\text{QAICc} \leq 2$; Table 1). *E. tetradonta* basal area had a clear positive relationship with habitat use; at sites with no *E. tetradonta* (0 m² ha⁻¹), northern quolls were unlikely to be detected (proportion of nights with detections at <0.01 [CI: 0.003–0.01]); at sites with the highest *E. tetradonta* basal area (25 m² ha⁻¹), northern quolls were an order of magnitude more likely to be detected (proportion of nights with detections at 0.11 [CI: 0.05–0.22]; Fig. 4a). Tree basal area (i.e. including all tree species) had a clear negative relationship with habitat use; at sites with the lowest tree basal area (10 m² ha⁻¹), northern quolls were more likely to be detected (proportion of nights with detections at 0.06 [CI: 0.03–0.10]); at sites with the highest

Table 1. Parameter inclusion for cat and northern quoll generalised linear models with a ΔQAICc of ≤ 2 .

Cat									
Model	Fire frequency	Total basal area	Elevation	Distance to plateau edge	NDVI	Distance to water	TRI	ΔQAICc	
1	+	+						0.0	
2	+	+	+					0.4	
3	+	+	+	+				1.1	
4	+	+			+			1.7	
5	+	+				+		1.9	
6	+	+		+				1.9	
w+	0.99	0.91	0.48	0.36	0.29	0.28	0.27		

Northern quoll									
Model	Fire frequency	Total basal area	<i>E. tetrodonta</i> basal area	Distance to plateau edge	NDVI	Distance to water	TRI	ΔQAICc	
1		+	+	+	+		+	0.0	
2		+	+	+	+	+	+	1.5	
3	+	+	+	+	+		+	1.6	
w+	0.32	0.99	0.99	0.99	0.90	0.33	0.99		

NDVI denotes normalised-difference vegetation index and TRI denotes topographic ruggedness index. ΔQAICc represents the difference between the model QAICc value and the top-ranking model; + represents parameter inclusion in the model; w+ represents the relative importance of each parameter using the sum of the Akaike weights, with bold w+ values indicating highly influential parameters.

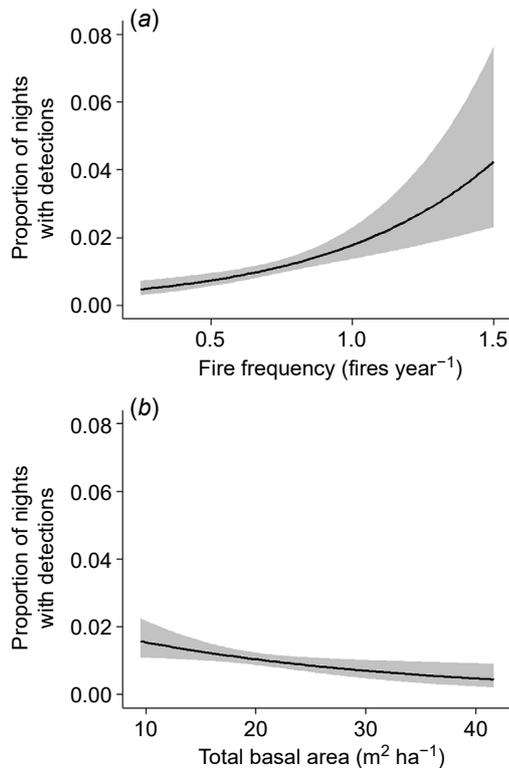


Fig. 3. The predicted relationship between the proportion of nights with detections of cats and the most supported predictor variables derived from a model averaged generalised linear model: (a) fire frequency and (b) total basal area. Gray bands represent the 95% confidence intervals of each prediction.

tree basal area ($40 \text{ m}^2 \text{ ha}^{-1}$), northern quolls were very unlikely to be detected (proportion of nights with detections at 0.002 [CI: 0.001–0.007]; Fig. 4b). Distance to plateau edge had a clear positive relationship with habitat use; at sites located furthest away from the plateau (1600 m), northern quolls were unlikely to be detected (proportion of nights with detections at 0.002 [CI: 0.001–0.01]); at sites close to the centre of the plateau (1400 m from the plateau edge), northern quolls were more likely to be detected (proportion of nights with detections at 0.07 [CI: 0.03–0.13]; Fig. 4c). Ruggedness had a clear positive relationship with habitat use; at flat sites with no ruggedness, northern quolls were unlikely to be detected (proportion of nights with detections at 0.01 [CI: 0.01–0.02]); at the most rugged sites, northern quolls were more likely to be detected (proportion of nights with detections at 0.07 [CI: 0.03–0.14]; Fig. 4d). NDVI had a clear positive relationship with habitat use; at sites with the lowest index value (0.42), northern quolls were unlikely to be detected (proportion of nights with detections at 0.008 [CI: 0.003–0.02]); at sites with the highest index value (0.74), northern quolls were more likely to be detected (proportion of nights with detections at 0.04 [CI: 0.02–0.07]; Fig. 4e).

Variation in habitat use by cats and northern quolls in relation to time-since-fire

Habitat use by cats and northern quolls was best explained by beta-binomial models including time-since-fire. For both species, the beta-binomial model containing time-since-fire had an AICc score >10 less than did the binomial model

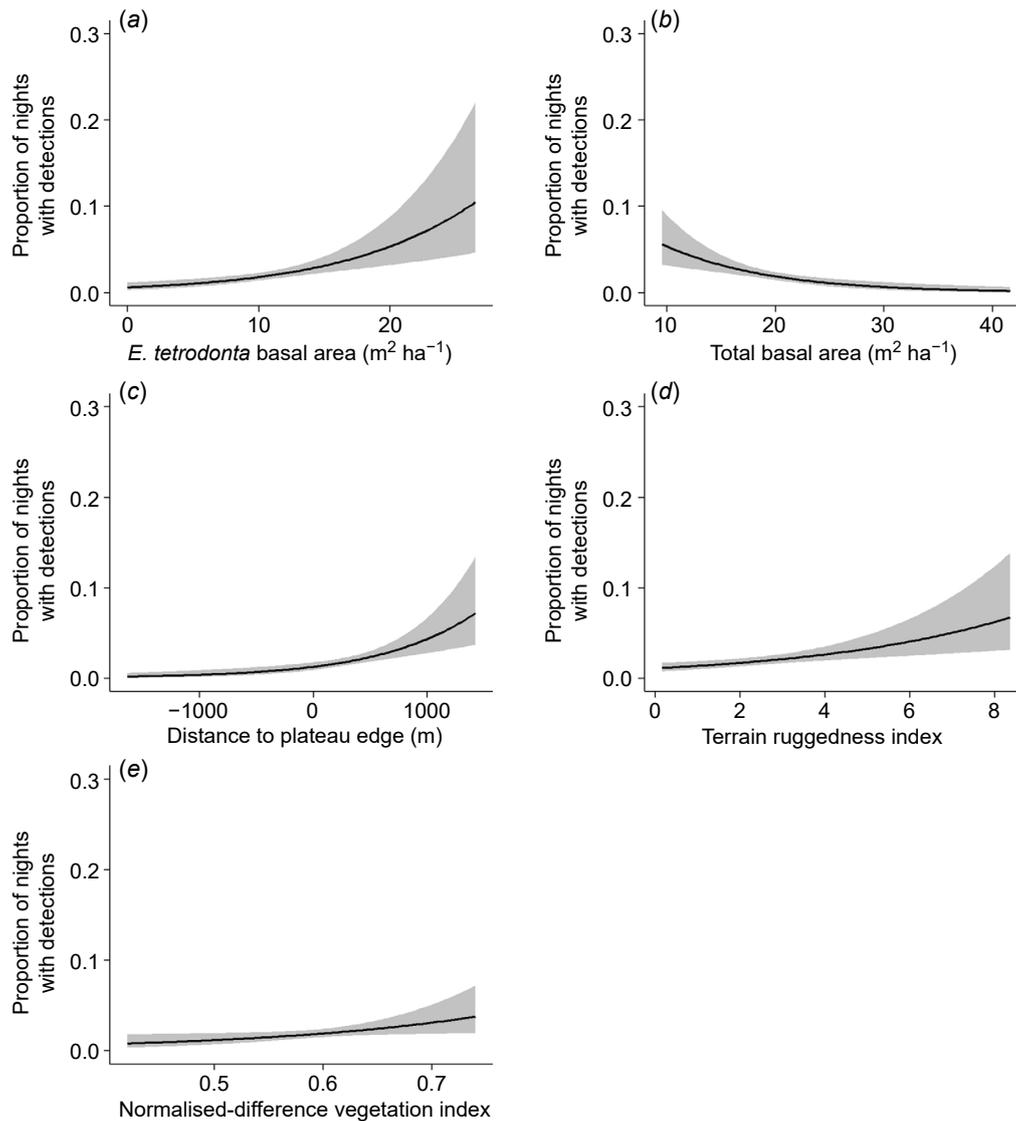


Fig. 4. The predicted relationship between the proportion of nights with detections of northern quolls and the most supported predictor variables derived from a model averaged generalised linear model: (a) *E. tetradonta* basal area, (b) total basal area, (c) distance to plateau edge, (d) terrain ruggedness index and (e) normalised-difference vegetation index. Gray bands represent the 95% confidence intervals of each prediction. Note that in c, negative numbers denote sites away from the plateau, and positive numbers denote sites atop of the plateau.

including time-since-fire and the null model. Cats did not show a clear relationship with time-since-fire, but trended towards a negative relationship (Fig. 2). In comparison, northern quolls showed a clear positive relationship with time-since-fire (Fig. 2).

Discussion

Remnant populations of the northern quoll on Cape York Peninsula have long been exposed to the main factors thought to be threatening small mammals across northern

Australia. Habitat conditions on the bauxite plateaux where these remnant populations occur are likely to have facilitated the persistence of northern quolls despite multiple threats, particularly predation by feral cats, which are locally abundant. Our findings highlighted a nexus among northern quolls, cats and fire, whereby naturally occurring fire refugia (in this case on the less frequently burnt plateau surfaces) benefit northern quolls by promoting structurally complex vegetation and, consequently, limiting habitat use by cats. This is consistent with a growing body of evidence showing that high fire frequency can promote cat activity and abundance, resulting in the decline of native mammals

susceptible to cat predation (McGregor *et al.* 2015, 2016; Davies *et al.* 2020; Stobo-Wilson *et al.* 2020b).

Cats appear to be associated with frequently burnt and structurally simple habitat at our study site. Our modelling showed that fire frequency had the strongest influence on habitat use by cats, with cats tending to use frequently burnt areas. Fires are most frequent in the surrounding low-lying open savanna, with the vegetation transition along the rugged edges of the plateau (from open savanna to dense *E. tetradonta* savanna) acting as a natural barrier to fire (Bowman 1986). Working in the savannas of the Kimberley and Cape York Peninsula regions, McGregor *et al.* (2015, 2016) showed that feral cats have improved hunting efficiency in open, grassland habitat and actively seek out recently burnt habitat, often far outside their established home ranges. We found that sites with the highest tree basal area had the lowest frequency of habitat use by cats. Given the findings of McGregor *et al.* (2015, 2016), it seems likely that the dense plateau vegetation limits the hunting efficiency of cats and, as a result, the suitability of these areas as habitat for cats. In addition to the immediate reduction in vegetation cover caused by fire, repeated fires at short intervals can reduce the structural complexity of tropical savanna communities over the long term (Williams *et al.* 1999; Russell-Smith *et al.* 2012; Woolley *et al.* 2018). Cats are likely to benefit from fire-driven reductions in the density and structural complexity of understorey vegetation (Davies *et al.* 2020; Stobo-Wilson *et al.* 2020b) to the detriment of small native mammals (Leahy *et al.* 2015; McDonald *et al.* 2016).

In contrast to the use of structurally simple habitat by cats, northern quolls most frequently used structurally complex, long-unburnt habitat. Our modelling found vegetation composition, ruggedness and time-since-fire had the strongest influence on habitat use by northern quolls. Northern quolls most frequently used the central areas of the plateaux; *E. tetradonta* basal area, NDVI and ruggedness were also significant positive predictors of northern quoll habitat use. *E. tetradonta* is known to be the primary den tree used by the northern quoll across the plateaux (G. J. Trewella, unpubl. data), and the strong association between northern quolls and *E. tetradonta* is most likely related to the high rate of hollow formation in this tree species, compared with other savanna trees (Werner and Prior 2007; Woolley *et al.* 2018). However, habitat use by northern quolls was negatively related to total tree basal area (i.e. including species other than *E. tetradonta*), with northern quolls infrequently using areas with high total tree basal area. Without considering the proportion of hollow-bearing trees in the landscape, high tree basal area alone may not provide necessary resources such as food and shelter to support a northern quoll population in habitat lacking other den resources, such as rock crevices. Similar to the findings of Moore *et al.* (2019), vegetation productivity, inferred from NDVI, was also correlated with habitat use by

northern quolls, with the most productive areas being used more frequently by northern quolls. The positive relationship between habitat use by northern quolls and ruggedness is consistent with a continent-wide pattern of remnant northern quoll populations being associated with rugged areas (Moore *et al.* 2019). Unlike for cats, we did not find a relationship between fire frequency and habitat use by northern quolls, but there was a strong association between northern quolls and long-unburnt habitat. Long-unburnt habitat in tropical savanna is likely to provide a greater cover from predation and have increased availability of denning resources such as hollow logs (Legge *et al.* 2008; Shaw *et al.* 2021), while also being avoided by cats (McGregor *et al.* 2014). These observed differences in habitat usage by northern quolls and cats highlight the importance of less frequently burnt refugia (such as bauxite plateaux on Cape York Peninsula) for the northern quoll across northern Australia.

A resource that appears to be a key determinant of persistence of northern quolls is den availability. Northern quolls are the largest marsupial that displays partial semelparity, with males dying following the annual breeding season (Dickman and Braithwaite 1992; Oakwood *et al.* 2001). This regular high population turnover means that annual recruitment and juvenile survivorship are vital to population persistence (Cremona *et al.* 2017; Moro *et al.* 2019). Ample availability of high-quality den resources (e.g. rock crevices, hollows in large trees and logs), that offer protection from threats during the vital joey-rearing phase, are likely to play a critical role in successful recruitment, and hence population persistence (Oakwood 2000). Where there is a choice of den resources, such as rock crevices or tree hollows, northern quolls have been reported to show a preference for rock crevices (Begg 1981; Oakwood 1997). As such, rocky refugia are seen as more suitable habitat for northern quoll, which can support higher quoll densities than can lowland savanna (Begg 1981; Schmitt *et al.* 1989; Oakwood 2002). However, savannas that lack rocky features can still provide sufficient den resources if large hollow-bearing trees, particularly hollow-forming species, such as *E. tetradonta* (Woolley *et al.* 2018), are abundant (Thomas *et al.* 2021). Reducing the frequency of high-intensity fires in tropical savannas is likely to promote the retention of large, hollow-bearing trees, which provide suitable den sites for northern quolls (Williams *et al.* 1999; Edwards *et al.* 2018; Woolley *et al.* 2018). Fire management strategies should therefore be targeted at maintaining structurally complex habitat, particularly through the retention of large hollow-bearing trees.

Despite demonstrating links between habitat conditions and patterns of habitat use by cats and northern quolls, we have not considered how their habitat use is likely to be affected by other species, most notably those whose abundances may have changed significantly in recent decades. Unfortunately, a lack of historical and contemporary surveys of mammals on Cape York Peninsula hinders our

ability to identify trends in species distributions and abundances in response to changes in land-management practices and biotic and abiotic processes through time. For example, we have not taken account of the potential role dingoes play, as apex predators, in regulating habitat use by cats and northern quolls (Glen *et al.* 2007; Hernandez-Santin *et al.* 2016; Cremona *et al.* 2017). Dingoes are common across the savannas of western Cape York Peninsula (Cairns *et al.* 2018); however, persecution by pastoralists, through poisoning and shooting, does occur. Whether this level of dingo persecution is enough to release cats from predation or competitive pressure, as predicted by mesopredator release theory (Ritchie and Johnson 2009; Kennedy *et al.* 2012), is worthy of consideration. Similarly, cat activity has been found to be highest in savannas where invasive herbivores are most abundant (Davies *et al.* 2020). Cattle pastoralism is a key industry on Cape York Peninsula; so, the simplification of vegetation through overgrazing is a widespread threat (Kutt and Woinarski 2007). Potential synergies between cats and livestock (both feral and managed) may be an important barrier to mammal conservation across Cape York Peninsula and elsewhere in northern Australia (Stobo-Wilson *et al.* 2020a).

Research over the past few decades has shown that northern Australian mammals are rapidly declining in response to a variety of threats, particularly predation by feral cats (Woinarski *et al.* 2011; Frank *et al.* 2014; Stobo-Wilson *et al.* 2020a). Given that the eradication of the cat is not currently feasible across unfenced landscapes, the maintenance of complex habitat may be one of the few ways to mitigate cat impacts on native mammals across northern Australia. Fire regimes appear to be a crucial factor determining whether populations of small mammals are able to persist in the extremely fire-prone savannas of northern Australia (Griffiths and Brook 2014; von Takach *et al.* 2022). Reductions in the frequency of fires, especially those of high intensity, can promote the persistence of large hollow-bearing trees (Williams *et al.* 1999; Edwards *et al.* 2018; Woolley *et al.* 2018) and potentially suppress cat activity (Davies *et al.* 2020; Stobo-Wilson *et al.* 2020b). However, achieving long-term reductions in fire frequency and intensity across the vast tropical savanna landscapes of northern Australia will also be a significant management challenge (Murphy and Russell-Smith 2010; Evans and Russell-Smith 2020; Russell-Smith *et al.* 2020). Prescribed burning in the early dry season (when fire-weather conditions are relatively benign compared to the late dry season) has been shown to be effective in reducing fire intensity (Price *et al.* 2012; Duncan *et al.* 2015; Radford *et al.* 2020, 2021), but typically does not reduce fire frequency. Hence, frequent prescribed burning can still negatively affect small mammal populations and promote cat activity (Andersen *et al.* 2005; Griffiths *et al.* 2015). These difficulties in fire management further emphasise the significance of bauxite plateaux as naturally occurring, less frequently burnt refugia, similar to

rocky refugia commonly found across northern Australia (Oakwood 2000; Hohnen *et al.* 2016; Moore *et al.* 2022). Despite these challenges, retaining structurally complex vegetation and suppressing cat activity through a low-frequency fire regime that promotes the retention of long-unburnt habitat is likely to have a significant benefit for northern quoll and threatened mammals across the tropical savannas of northern Australia.

References

- Abbott I (2008) The spread of the cat, *Felis catus*, in Australia: re-examination of the current conceptual model with additional information. *Conservation Science Western Australia* 7, 1–17.
- Andersen AN, Cook GD, Corbett LK, Douglas MM, Eager RW, Russell-Smith J, Setterfield SA, Williams RJ, Woinarski JCZ (2005) Fire frequency and biodiversity conservation in Australian tropical savannas: implications from the Kapalga fire experiment. *Austral Ecology* 30, 155–167. doi:10.1111/j.1442-9993.2005.01441.x
- Australian Bureau of Meteorology (2021) Average annual, seasonal and monthly rainfall. Available at <http://www.bom.gov.au/climate/data/index.shtml> [Accessed 01 February 2023]
- Baker CM, Bode M (2016) Placing invasive species management in a spatiotemporal context. *Ecological Applications* 26, 712–725. doi:10.1890/15-0095
- Bartoń K (2020) MuMIn: multi-model inference (version 1.46.0). Available at <https://cran.r-project.org/web/packages/MuMIn/MuMIn.pdf> [Accessed 24 February 2022]
- Begg RJ (1981) The small mammals of Little Nourlangie Rock, N.T. III. Ecology of *Dasyurus hallucatus*, the northern quoll (Marsupialia: Dasyuridae). *Wildlife Research* 8, 73–85. doi:10.1071/WR9810073
- Blackburn TM, Cassey P, Duncan RP, Evans KL, Gaston KJ (2004) Avian extinction and mammalian introductions on oceanic islands. *Science* 305, 1955–1958. doi:10.1126/science.1101617
- Bodey TW, Bearhop S, McDonald RA (2011) Localised control of an introduced predator: creating problems for the future? *Biological Invasions* 13, 2817–2828. doi:10.1007/s10530-011-9965-2
- Bowman DMJS (1986) Stand characteristics, understorey associates and environmental correlates of *Eucalyptus tetrodonta* F.Muell. forests on Gunn Point, northern Australia. *Vegetatio* 65, 105–113. doi:10.1007/BF00044881
- Bowman DMJS, Fensham RJ (1991) Response of a monsoon forest–savanna boundary to fire protection, Weipa, northern Australia. *Austral Ecology* 16, 111–118. doi:10.1111/j.1442-9993.1991.tb01486.x
- Braithwaite RW, Griffiths AD (1994) Demographic variation and range contraction in the northern quoll, *Dasyurus hallucatus* (Marsupialia: Dasyuridae). *Wildlife Research* 21, 203–217. doi:10.1071/WR9940203
- Brooks ME, Kristensen K, Benthem KJvan, Magnusson A, Berg CW, Nielsen A, Skaug HJ, Mächler M, Bolker BM (2017) glmmTMB balances speed and flexibility among packages for zero-inflated generalized linear mixed modeling. *The R Journal* 9, 378–400. doi:10.32614/RJ-2017-066
- Burnett S (1997) Colonizing Cane Toads cause population declines in native predators: reliable anecdotal information and management implications. *Pacific Conservation Biology* 3, 65–72. doi:10.1071/PC970065
- Burnham KP, Anderson DR (Eds) (1998) ‘Model selection and multimodel inference: a practical information-theoretic approach.’ (Springer: New York, NY, USA)
- Cáceres CE, Knight CJ, Hall SR (2009) Predator–spreaders: predation can enhance parasite success in a planktonic host–parasite system. *Ecology* 90, 2850–2858. doi:10.1890/08-2154.1
- Cairns KM, Shannon LM, Koler-Matznick J, Ballard JWO, Boyko AR (2018) Elucidating biogeographical patterns in Australian native canids using genome wide SNPs. *PLoS ONE* 13, e0198754. doi:10.1371/journal.pone.0198754
- Campbell KJ, Harper G, Algar D, Hanson CC, Keitt BS, Robinson S (2011) Review of feral cat eradications on islands. In ‘Island invasives: eradication and management: proceedings of the International

- Conference on Island Invasives'. (Eds CR Veitch, MN Clout, DR Towns) pp. 37–46. (IUCN: Gland, Switzerland)
- Castle G, Smith D, Allen LR, Allen BL (2021) Terrestrial mesopredators did not increase after top-predator removal in a large-scale experimental test of mesopredator release theory. *Scientific Reports* **11**, 18205. doi:10.1038/s41598-021-97634-4
- Clout MN, Russell JC, Clout MN, Russell JC (2008) The invasion ecology of mammals: a global perspective. *Wildlife Research* **35**, 180–184. doi:10.1071/WR07091
- Covacevich J, Archer M (1975) The distribution of the cane toad, *Bufo marinus*, in Australia and its effects on indigenous vertebrates. *Memoirs of the Queensland Museum* **17**, 305–310.
- Cremona T, Crowther MS, Webb JK (2017) High mortality and small population size prevent population recovery of a reintroduced mesopredator. *Animal Conservation* **20**, 555–563. doi:10.1111/acv.12358
- Crossman S, Li O (2015) Surface hydrology lines (Regional). (Geoscience Australia: Canberra) Available at <http://pid.geoscience.gov.au/dataset/ga/83107> [Accessed 20 July 2021]
- Davies HF, Maier SW, Murphy BP (2020) Feral cats are more abundant under severe disturbance regimes in an Australian tropical savanna. *Wildlife Research* **47**, 624–632. doi:10.1071/WR19198
- Department of Natural Resources, Mines and Energy (2018a) Digital elevation model - 3 second - Queensland. State of Queensland. Available at <https://www.data.qld.gov.au/dataset/digital-elevation-model-3-second-queensland> [Accessed 1 February 2023]
- Department of Natural Resources, Mines and Energy (2018b) Vegetation management regional ecosystem map - version 12.02. State of Queensland. Available at <https://www.data.qld.gov.au/dataset/vegetation-management-act-series/resource/7fbb5561-7417-405f-8622-a4799687903ba4799687903b> [Accessed 01 February 2023]
- Dickman CR, Braithwaite RW (1992) Postmating mortality of males in the dasyurid marsupials, *Dasyurus* and *Parantechinus*. *Journal of Mammalogy* **73**, 143–147. doi:10.2307/1381875
- Doherty TS, Bengsen AJ, Davis RA (2014) A critical review of habitat use by feral cats and key directions for future research and management. *Wildlife Research* **41**, 435–446. doi:10.1071/WR14159
- Doherty TS, Dickman CR, Nimmo DG, Ritchie EG (2015) Multiple threats, or multiplying the threats? Interactions between invasive predators and other ecological disturbances. *Biological Conservation* **190**, 60–68. doi:10.1016/j.biocon.2015.05.013
- Doherty TS, Glen AS, Nimmo DG, Ritchie EG, Dickman CR (2016) Invasive predators and global biodiversity loss. *Proceedings of the National Academy of Sciences* **113**, 11261–11265. doi:10.1073/pnas.1602480113
- Doherty TS, Dickman CR, Johnson CN, Legge SM, Ritchie EG, Woinarski JCZ (2017) Impacts and management of feral cats *Felis catus* in Australia. *Mammal Review* **47**, 83–97. doi:10.1111/mam.12080
- Doherty TS, Davis NE, Dickman CR, Forsyth DM, Letnic M, Nimmo DG, Palmer R, Ritchie EG, Benshemesh J, Edwards G, Lawrence J, Lumsden L, Pascoe C, Sharp A, Stokeld D, Myers C, Story G, Story P, Triggs B, Venosta M, Wysong M, Newsome TM (2019) Continental patterns in the diet of a top predator: Australia's dingo. *Mammal Review* **49**, 31–44. doi:10.1111/mam.12139
- Dueñas M-A, Hemming DJ, Roberts A, Diaz-Soltero H (2021) The threat of invasive species to IUCN-listed critically endangered species: a systematic review. *Global Ecology and Conservation* **26**, e01476. doi:10.1016/j.gecco.2021.e01476
- Duncan BW, Schmalzer PA, Breininger DR, Stolen ED (2015) Comparing fuels reduction and patch mosaic fire regimes for reducing fire spread potential: a spatial modeling approach. *Ecological Modelling* **314**, 90–99. doi:10.1016/j.ecolmodel.2015.07.013
- Dunlop JA, Rayner K, Doherty TS (2017) Dietary flexibility in small carnivores: a case study on the endangered northern quoll, *Dasyurus hallucatus*. *Journal of Mammalogy* **98**, 858–866. doi:10.1093/jmammal/gyx015
- Edwards AC, Russell-Smith J, Maier SW (2018) A comparison and validation of satellite-derived fire severity mapping techniques in fire prone north Australian savannas: extreme fires and tree stem mortality. *Remote Sensing of Environment* **206**, 287–299. doi:10.1016/j.rse.2017.12.038
- European Space Agency (2021) Sentinel-2 remote sensing data. Available at <https://apps.sentinel-hub.com/eo-browser/> [Accessed 20 July 2021]
- Evans J, Russell-Smith J (2020) Delivering effective savanna fire management for defined biodiversity conservation outcomes: an Arnhem Land case study. *International Journal of Wildland Fire* **29**, 386–400. doi:10.1071/WF18126
- Fancourt BA, Cremasco P, Wilson C, Gentle MN (2019) Do introduced apex predators suppress introduced mesopredators? A multiscale spatiotemporal study of dingoes and feral cats in Australia suggests not. *Journal of Applied Ecology* **56**, 2584–2595. doi:10.1111/1365-2664.13514
- Frank ASK, Johnson CN, Potts JM, Fisher A, Lawes MJ, Woinarski JCZ, Tuft K, Radford LJ, Gordon LJ, Collis M-A, 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. doi:10.1111/1365-2664.12323
- Glen AS, Dickman CR, Soulé ME, Mackey BG (2007) Evaluating the role of the dingo as a trophic regulator in Australian ecosystems. *Austral Ecology* **32**, 492–501. doi:10.1111/j.1442-9993.2007.01721.x
- Griffiths AD, Brook BW (2014) Effect of fire on small mammals: a systematic review. *International Journal of Wildland Fire* **23**, 1034–1043. doi:10.1071/WF14026
- Griffiths AD, Garnett ST, Brook BW (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. doi:10.1016/j.biocon.2015.03.021
- Hernandez-Santin L, Goldizen AW, Fisher DO (2016) Introduced predators and habitat structure influence range contraction of an endangered native predator, the northern quoll. *Biological Conservation* **203**, 160–167. doi:10.1016/j.biocon.2016.09.023
- Hohnen R, Tuft K, Legge S, Walters N, Johanson L, Carver S, Radford LJ, Johnson CN (2016) The significance of topographic complexity in habitat selection and persistence of a declining marsupial in the Kimberley region of Western Australia. *Australian Journal of Zoology* **64**, 198–216. doi:10.1071/ZO16015
- Holmes ND, Spatz DR, Opper S, Tershy B, Croll DA, Keitt B, Genovesi P, Burfield IJ, Will DJ, Bond AL, Wegmann A, Aguirre-Muñoz A, Raine AF, Knapp CR, Hung C-H, Wingate D, Hagen E, Méndez-Sánchez F, Rocamora G, Yuan H-W, Fric J, Millett J, Russell J, Liske-Clark J, Vidal E, Jourdan H, Campbell K, Springer K, Swinnerton K, Gibbons-Decherong L, Langrand O, Brooke MdeL, McMinn M, Bunbury N, Oliveira N, Sposimo P, Geraldes P, McClelland P, Hodum P, Ryan PG, Borroto-Páez R, Pierce R, Griffiths R, Fisher RN, Wanless R, Pasachnik SA, Cranwell S, Micol T, Butchart SHM (2019) Globally important islands where eradicating invasive mammals will benefit highly threatened vertebrates. *PLoS ONE* **14**, e0212128. doi:10.1371/journal.pone.0212128
- Jones HP, Holmes ND, Butchart SHM, Tershy BR, Kappes PJ, Corkery I, Aguirre-Muñoz A, Armstrong DP, Bonnaud E, Burbidge AA, Campbell K, Courchamp F, Cowan PE, Cuthbert RJ, Ebbert S, Genovesi P, Howald GR, Keitt BS, Kress SW, Miskelly CM, Opper S, Poncet S, Rauzon MJ, Rocamora G, Russell JC, Samaniego-Herrera A, Seddon PJ, Spatz DR, Towns DR, Croll DA (2016) Invasive mammal eradication on islands results in substantial conservation gains. *Proceedings of the National Academy of Sciences* **113**, 4033–4038. doi:10.1073/pnas.1521179113
- Kennedy M, Phillips BL, Legge S, Murphy SA, Faulkner RA (2012) Do dingoes suppress the activity of feral cats in northern Australia? *Austral Ecology* **37**, 134–139. doi:10.1111/j.1442-9993.2011.02256.x
- Kreplins TL, Kennedy MS, O'Leary RA, Adams PJ, Dundas SJ, Fleming PA (2021) Fighting like cats and dogs? Dingoes do not constrain spatial and temporal movements of feral cats. *Food Webs* **27**, e00173. doi:10.1016/j.fooweb.2020.e00173
- Kutt AS, Woinarski JCZ (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. doi:10.1017/S0266467406003579
- Lazenby BT, Mooney NJ, Dickman CR (2014) Effects of low-level culling of feral cats in open populations: a case study from the forests of southern Tasmania. *Wildlife Research* **41**, 407–420. doi:10.1071/WR14030

- Leahy L, Legge SM, Tuft K, McGregor HW, Barmuta LA, Jones ME, Johnson CN (2015) Amplified predation after fire suppresses rodent populations in Australia's tropical savannas. *Wildlife Research* **42**, 705–716. doi:10.1071/WR15011
- Leblanc M, Tweed S, Lyon BJ, Bailey J, Franklin CE, Harrington G, Suckow A (2015) On the hydrology of the bauxite oases, Cape York Peninsula, Australia. *Journal of Hydrology* **528**, 668–682. doi:10.1016/j.jhydrol.2015.06.001
- Legge S, Murphy S, Heathcote J, Flaxman E, Augusteyn 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. doi:10.1071/WR07016
- Legge S, Woinarski JCZ, Burbidge AA, Palmer R, Ringma J, Radford JQ, Mitchell N, Bode M, Wintle B, Baseler M, Bentley J, Copley P, Dexter N, Dickman CR, Gillespie GR, Hill B, Johnson CN, Latch P, Letnic M, Manning A, McCreless EE, Menkhorst P, Morris K, Moseby K, Page M, Pannell D, Tuft K (2018) Havens for threatened Australian mammals: the contributions of fenced areas and offshore islands to the protection of mammal species susceptible to introduced predators. *Wildlife Research* **45**, 627–644. doi:10.1071/WR17172
- Legge S, Woinarski JCZ, Dickman CR, Doherty TS, McGregor H, Murphy BP (2020) Cat ecology, impacts and management in Australia. *Wildlife Research* **47**, i–vi. doi:10.1071/WRv47n8_ED
- Letnic M, Koch F, Gordon C, Crowther MS, Dickman CR (2009) Keystone effects of an alien top-predator stem extinctions of native mammals. *Proceedings: Biological Sciences* **276**, 3249–3256. doi:10.1098/rspb.2009.0574
- Letnic M, Ritchie EG, Dickman CR (2012) Top predators as biodiversity regulators: the dingo *Canis lupus dingo* as a case study. *Biological Reviews* **87**, 390–413. doi:10.1111/j.1469-185X.2011.00203.x
- Long JL (2003) 'Introduced mammals of the world: their history, distribution and influence.' (CSIRO Publishing)
- McDonald PJ, Stewart A, Schubert AT, Nano CEM, Dickman CR, Luck GW (2016) Fire and grass cover influence occupancy patterns of rare rodents and feral cats in a mountain refuge: implications for management. *Wildlife Research* **43**, 121–129. doi:10.1071/WR15220
- McDonald PJ, Stewart A, Jensen MA, McGregor HW (2020) Topographic complexity potentially mediates cat predation risk for a critically endangered rodent. *Wildlife Research* **47**, 643–648. doi:10.1071/WR19172
- McGregor HW, Legge S, Jones ME, Johnson CN (2014) Landscape management of fire and grazing regimes alters the fine-scale habitat utilisation by feral cats. *PLoS ONE* **9**, e109097. doi:10.1371/journal.pone.0109097
- McGregor H, Legge S, Jones ME, Johnson CN (2015) Feral cats are better killers in open habitats, revealed by animal-borne video. *PLoS ONE* **10**, e0133915. doi:10.1371/journal.pone.0133915
- McGregor HW, Cliff HB, Kanowski J (2016) Habitat preference for fire scars by feral cats in Cape York Peninsula, Australia. *Wildlife Research* **43**, 623–633. doi:10.1071/WR16058
- Miritis V, Rendall AR, Doherty TS, Coetsee AL, Ritchie EG (2020) Living with the enemy: a threatened prey species coexisting with feral cats on a fox-free island. *Wildlife Research* **47**, 633–642. doi:10.1071/WR19202
- Moore HA, Dunlop JA, Valentine LE, Woinarski JCZ, Ritchie EG, Watson DM, Nimmo DG (2019) Topographic ruggedness and rainfall mediate geographic range contraction of a threatened marsupial predator. *Diversity and Distributions* **25**, 1818–1831. doi:10.1111/ddi.12982
- Moore HA, Dunlop JA, Jolly CJ, Kelly E, Woinarski JCZ, Ritchie EG, Burnett S, van Leeuwen S, Valentine LE, Cowan MA, Nimmo DG (2022) A brief history of the northern quoll (*Dasyurus hallucatus*): a systematic review. *Australian Mammalogy* **44**, 185–207. doi:10.1071/AM21002
- Moro D, Dunlop J, Williams MR (2019) Northern quoll persistence is most sensitive to survivorship of juveniles. *Wildlife Research* **46**, 165–175. doi:10.1071/WR18010
- Moseby KE, Read JL, Galbraith B, Munro N, Newport J, Hill BM (2011) The use of poison baits to control feral cats and red foxes in arid South Australia II. Bait type, placement, lures and non-target uptake. *Wildlife Research* **38**, 350–358. doi:10.1071/WR10236
- Murphy BP, Russell-Smith J (2010) Fire severity in a northern Australian savanna landscape: the importance of time since previous fire. *International Journal of Wildland Fire* **19**, 46–51. doi:10.1071/WF08202
- North Australian Fire Information (2021) *North Australian 250m fire frequency mapping 2000 to 2021*. Available at <https://firenorth.org.au/nafi3/> [Accessed 20 July 2021]
- Oakwood M (1997) The ecology of the northern quoll, *Dasyurus hallucatus*. PhD thesis, Australian National University, Canberra, ACT, Australia.
- Oakwood M (2000) Reproduction and demography of the northern quoll, *Dasyurus hallucatus*, in the lowland savanna of northern Australia. *Australian Journal of Zoology* **48**, 519–539. doi:10.1071/ZO00028
- Oakwood M (2002) Spatial and social organization of a carnivorous marsupial *Dasyurus hallucatus* (Marsupialia: Dasyuridae). *Journal of Zoology* **257**, 237–248. doi:10.1017/S0952836902000833
- Oakwood M, Bradley AJ, Cockburn A (2001) Semelparity in a large marsupial. *Proceedings of the Royal Society of London. Series B: Biological Sciences* **268**, 407–411. doi:10.1098/rspb.2000.1369
- Oakwood M, Woinarski JCZ, Burnett S (2016) *Dasyurus hallucatus*. The IUCN Red List of Threatened Species 2016 [Online]. Available at <https://dx.doi.org/10.2305/IUCN.UK.2016-2.RLTS.T6295A21947321.en>
- Parkes J, Fisher P, Robinson S, Aguirre-Muñoz A (2014) Eradication of feral cats from large islands: an assessment of the effort required for success. *New Zealand Journal of Ecology* **38**, 307–314.
- Price OF, Russell-Smith J, Watt F (2012) The influence of prescribed fire on the extent of wildfire in savanna landscapes of western Arnhem Land, Australia. *International Journal of Wildland Fire* **21**, 297–305. doi:10.1071/WF10079
- Radford IJ, Woolley L-A, Corey B, Vigilante T, Wunambal Gaambera Aboriginal Corporation, Hatherley E, Fairman R, Carnes K, Start AN (2020) Prescribed burning benefits threatened mammals in northern Australia. *Biodiversity and Conservation* **29**, 2985–3007. doi:10.1007/s10531-020-02010-9
- Radford IJ, Corey B, Carnes K, Shedley E, McCaw L, Woolley L-A (2021) Landscape-scale effects of fire, cats, and feral livestock on threatened savanna mammals: unburnt habitat matters more than pyrodiversity. *Frontiers in Ecology and Evolution* **9**, 739817. doi:10.3389/fevo.2021.739817
- R Core Team (2020) 'R: a language and environment for statistical computing.' (R Foundation for Statistical Computing: Vienna, Austria) Available at <https://www.R-project.org/> [Accessed 28 February 2022]
- Read JL, Bengsen AJ, Meek PD, Moseby KE (2015) How to snap your cat: optimum lures and their placement for attracting mammalian predators in arid Australia. *Wildlife Research* **42**, 1–12. doi:10.1071/WR14193
- Riley SJ, Degloria SD, Elliot R (1999) A terrain ruggedness index that quantifies topographic heterogeneity. *Intermountain Journal of Science* **5**, 23–27.
- Risbey DA, Calver M, Short J (1997) Control of feral cats for nature conservation. I. Field tests of four baiting methods. *Wildlife Research* **24**, 319–326. doi:10.1071/WR96051
- Ritchie EG, Johnson CN (2009) Predator interactions, mesopredator release and biodiversity conservation. *Ecology Letters* **12**, 982–998. doi:10.1111/j.1461-0248.2009.01347.x
- Russell-Smith J, Edwards AC, Price OF (2012) Simplifying the savanna: the trajectory of fire-sensitive vegetation mosaics in northern Australia. *Journal of Biogeography* **39**, 1303–1317. doi:10.1111/j.1365-2699.2012.02679.x
- Russell-Smith J, Edwards AC, Sangha KK, Yates CP, Gardener MR (2020) Challenges for prescribed fire management in Australia's fire-prone rangelands: the example of the Northern Territory. *International Journal of Wildland Fire* **29**, 339–353. doi:10.1071/WF18127
- Schmitt LH, Bradley AJ, Kemper CM, Kitchener DJ, Humphreys WF, How RA (1989) Ecology and physiology of the northern quoll, *Dasyurus hallucatus* (Marsupialia, Dasyuridae), at Mitchell Plateau, Kimberley, Western Australia. *Journal of Zoology* **217**, 539–558. doi:10.1111/j.1469-7998.1989.tb02510.x
- Shaw RE, James AI, Tuft K, Legge S, Cary GJ, Peakall R, Banks SC (2021) Unburnt habitat patches are critical for survival and *in situ* population recovery in a small mammal after fire. *Journal of Applied Ecology* **58**, 1325–1335. doi:10.1111/1365-2664.13846

- Sih A, Bolnick DI, Luttbeg B, Orrock JL, Peacor SD, Pintor LM, Preisser E, Rehg JS, Vonesh JR (2010) Predator–prey naïveté, antipredator behavior, and the ecology of predator invasions. *Oikos* **119**, 610–621. doi:10.1111/j.1600-0706.2009.18039.x
- Specht RL, Salt RB, Reynolds ST (1977) Vegetation in the vicinity of Weipa, north Queensland. *Proceedings of the Royal Society of Queensland* **88**, 17–38.
- Stobo-Wilson AM, Stokeld D, Einoder LD, Davies HF, Fisher A, Hill BM, Mahney T, Murphy BP, Scroggie MP, Stevens A, Woinarski JCZ, Bawinanga Rangers, Warddeken Rangers, Gillespie GR (2020a) Bottom-up and top-down processes influence contemporary patterns of mammal species richness in Australia's monsoonal tropics. *Biological Conservation* **247**, 108638. doi:10.1016/j.biocon.2020.108638
- Stobo-Wilson AM, Stokeld D, Einoder LD, Davies HF, Fisher A, Hill BM, Mahney T, Murphy BP, Stevens A, Woinarski JCZ, Rangers B, Rangers W, Gillespie GR (2020b) Habitat structural complexity explains patterns of feral cat and dingo occurrence in monsoonal Australia. *Diversity and Distributions* **26**, 832–842. doi:10.1111/ddi.13065
- Stokeld D, Frank ASK, Hill B, Choy JL, Mahney T, Stevens A, Young S, Rangers D, Rangers W, Gillespie GR (2015) Multiple cameras required to reliably detect feral cats in northern Australian tropical savanna: an evaluation of sampling design when using camera traps. *Wildlife Research* **42**, 642–649. doi:10.1071/WR15083
- Symonds MRE, Moussalli A (2011) A brief guide to model selection, multimodel inference and model averaging in behavioural ecology using Akaike's information criterion. *Behavioral Ecology and Sociobiology* **65**, 13–21. doi:10.1007/s00265-010-1037-6
- Tannerfeldt M, Elmhagen B, Angerbjörn A (2002) Exclusion by interference competition? The relationship between red and arctic foxes. *Oecologia* **132**, 213–220. doi:10.1007/s00442-002-0967-8
- Thomas H, Cameron SF, Campbell HA, Micheli-Campbell MA, Kirke EC, Wheatley R, Wilson RS (2021) Rocky escarpment versus savanna woodlands: comparing diet and body condition as indicators of habitat quality for the endangered northern quoll (*Dasyurus hallucatus*). *Wildlife Research* **48**, 434–443. doi:10.1071/WR20032
- Ujvari B, Oakwood M, Madsen T (2013) Queensland northern quolls are not immune to cane toad toxin. *Wildlife Research* **40**, 228–231. doi:10.1071/WR13011
- Van Dyck S, Strahan R (Eds) (2008) 'The mammals of Australia.' (New Holland Publishers: Sydney, NSW, Australia)
- von Takach B, Jolly CJ, Dixon KM, Penton CE, Doherty TS, Banks SC (2022) Long-unburnt habitat is critical for the conservation of threatened vertebrates across Australia. *Landscape Ecology* **37**, 1469–1482. doi:10.1007/s10980-022-01427-7
- Wenger KF (Ed.) (1984) 'Forestry handbook.' (Wiley: New York, NY, USA)
- Werner PA, Prior LD (2007) Tree-piping termites and growth and survival of host trees in savanna woodland of north Australia. *Journal of Tropical Ecology* **23**, 611–622. doi:10.1017/S0266467407004476
- Williams RJ, Cook GD, Gill AM, Moore PHR (1999) Fire regime, fire intensity and tree survival in a tropical savanna in northern Australia. *Austral Ecology* **24**, 50–59. doi:10.1046/j.1442-9993.1999.00946.x
- Winter JW, Atherton RG (1985) 'Survey of the mammals and other vertebrates of the Weipa region, Cape York Peninsula.' (Queensland National Parks and Wildlife Service: Brisbane, QLD, Australia)
- Woinarski JCZ, Armstrong M, Brennan K, Fisher A, Griffiths AD, Hill B, Milne DJ, Palmer C, Ward S, Watson M, Winderlich S, Young S (2010) Monitoring indicates rapid and severe decline of native small mammals in Kakadu National Park, northern Australia. *Wildlife Research* **37**, 116–126. doi:10.1071/WR09125
- Woinarski JCZ, Legge S, Fitzsimons JA, Traill BJ, Burbidge AA, Fisher A, Firth RSC, Gordon IJ, Griffiths AD, Johnson CN, McKenzie NL, Palmer C, Radford I, Rankmore B, Ritchie EG, Ward S, Ziemicki M (2011) The disappearing mammal fauna of northern Australia: context, cause, and response: disappearing mammal fauna of north Australia. *Conservation Letters* **4**, 192–201. doi:10.1111/j.1755-263X.2011.00164.x
- Woinarski JCZ, Braby MF, Burbidge AA, Coates D, Garnett ST, Fensham RJ, Legge SM, McKenzie NL, Silcock JL, Murphy BP (2019) Reading the black book: the number, timing, distribution and causes of listed extinctions in Australia. *Biological Conservation* **239**, 108261. doi:10.1016/j.biocon.2019.108261
- Woolley L-A, Murphy BP, Radford IJ, Westaway J, Woinarski JCZ (2018) Cyclones, fire, and termites: the drivers of tree hollow abundance in northern Australia's mesic tropical savanna. *Forest Ecology and Management* **419–420**, 146–159. doi:10.1016/j.foreco.2018.03.034
- Zuur AF, Ieno EN, Elphick CS (2010) A protocol for data exploration to avoid common statistical problems. *Methods in Ecology and Evolution* **1**, 3–14. doi:10.1111/j.2041-210X.2009.00001.x

Data availability. The data that support this study will be shared upon reasonable request to the corresponding author.

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