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Habitat structural complexity explains patterns of feral cat and dingo occurrence in monsoonal Australia

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Abstract

Aim: An interaction between reduced habitat structural complexity and predation by feral cats (*Felis catus*) has been hypothesized as the primary driver of mammal decline in northern Australia. However, we have a limited understanding of the drivers of the distribution and abundance of feral cats at a landscape scale, including whether the occurrence of a top predator, the dingo (*Canis familiaris* [dingo]), limits feral cat populations. We modelled feral cat and dingo site occurrence, to provide the first broad-scale assessment of their distributional patterns and co-occurrence within monsoonal Australia.

Location: About 370,000 km² of monsoonal area in the Northern Territory.

Methods: We surveyed 376 sites using camera traps. We used single- and two-species occupancy models to investigate feral cat and dingo site occurrence and the influence of dingoes on feral cat occupancy. We included predictor variables that relate to hypotheses of predator occurrence, including both environmental and disturbance-related variables.

Results: Feral cat occurrence and dingo occurrence were best predicted by indices of habitat structural complexity; feral cat occurrence declined with increasing productivity, except in areas of relatively high fire activity (fire frequency and extent), and dingo occurrence declined with terrain ruggedness. We found no evidence that dingoes are spatially limiting feral cat occurrence.

Main conclusions: Our findings suggest the protection and enhancement of habitat structural complexity at both the local and landscape scale could enable conservation managers to reduce the exposure of small- and medium-sized mammals to feral cats and dingoes. This can most likely be achieved through improved fire and feral herbivore management, which is a more feasible management option than lethal predator control.

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KEY WORDS

critical weight range, mammal decline, northern Australia, occupancy model, predators, top predator

1 | INTRODUCTION

Australia has experienced a higher rate of mammal extinction than any other country, with ongoing declines of many native mammal species (Woinarski, Burbidge, & Harrison, 2015). In contrast to global patterns, mammal declines in Australia have been concentrated in remote regions (Woinarski et al., 2015). More recently, marked declines of a wide range of small- and medium-sized mammals have been reported in northern Australia's tropical savannas (Woinarski, Legge, et al., 2011). Identifying drivers of decline has been challenging due to uncertainty around when declines first began; the vast and remote region in which the declines have occurred; and the subtle, interacting landscape changes that have occurred since European arrival (Woinarski, Legge, et al., 2011). These challenges have also severely hampered our ability to develop effective management strategies.

Given the limited extent and duration of long-term monitoring in northern Australia, identified patterns of mammal decline in the region have instead been used to infer potential drivers. One identified pattern is the disproportionate decline of "critical weight range" (CWR; 35–5,000 g body mass) mammals (Murphy & Davies, 2014; Woinarski, 2015). Similar declines in ground-dwelling CWR mammals were first observed in arid and semi-arid Australia and have been primarily attributed to predation by the introduced feral cat (*Felis catus*) and red fox (*Vulpes vulpes*; Burbidge & McKenzie, 1989; Short & Smith, 1994). In the absence of the red fox in northern Australia, the decline of the region's CWR mammals suggests that predation by feral cats may be a leading cause of, or at least a contributing factor to, decline. The hypothesis is further supported by the persistence of some declining species on cat-free islands neighbouring mainland northern Australia (Southgate et al., 1996), and the disappearance of species once feral cats have been introduced (Woinarski, Ward, et al., 2011).

An additional pattern of decline is the loss of several CWR mammals from areas of low rainfall, with a resulting contraction to the mesic ends of their former distribution (McKenzie, 1981; Start, Burbidge, McKenzie, & Palmer, 2007). In northern Australia, high rainfall areas are more productive and have greater tree species richness, tree height, canopy cover and basal area, compared to areas of low rainfall (Williams, Duff, Bowman, & Cook, 1996). The relatively greater persistence of mammals in areas of high rainfall could be in response to either greater productivity, and therefore food availability, and/or greater structural complexity of habitat, and therefore shelter. Several species have also been lost from the lowland portion of their former range and now only persist in relatively rugged upland regions (e.g., Start et al., 2007), indicating a correlation between greater habitat structural complexity (from either high productivity or ruggedness) and mammal persistence in northern Australia.

Neither predation by feral cats, or changes to habitat structural complexity, can alone explain the geographic pattern of decline of CWR mammals. However, building on these patterns of decline, an interaction between reduced habitat structural complexity and predation by feral cats has been hypothesized as the primary driver of CWR mammal decline in northern Australia (Allen, 2011; Legge et al., 2019; McGregor, Cliff, & Kanowski, 2016). This hypothesis predicts that feral cats are more likely to occur in areas of low habitat structural complexity, as they are advantaged by disturbances that remove or simplify vegetation cover, such as frequent and/or severe fires and overgrazing by large introduced herbivores. There are two major lines of evidence to support this, the first being that altered fire regimes (increased fire frequency and severity) and overgrazing by introduced herbivores since European arrival have potentially modified habitat structural complexity almost pervasively across northern Australia. A greater frequency of fire, especially of high-severity fires, reduces habitat structural complexity by removing ground cover and reducing the shrubby mid-storey (Russell-Smith, Edwards, & Price, 2012; Williams, Cook, Gill, & Moore, 1999). The impact of altered fire regimes is especially evident in areas of relatively low rainfall as there is already a naturally open and simple habitat structure (Williams et al., 1996). Additionally, heavy grazing by livestock and large introduced herbivores removes the grassy understorey (Sharp & Whittaker, 2003). These disturbances have the capacity to alter habitat structure in a way that removes cover for CWR mammals making them more vulnerable to predation. The negative impact of such disturbances is supported by fewer CWR mammal populations in areas with large, frequent fires (Lawes et al., 2015) and an increase in CWR mammal abundance following the removal of introduced herbivores (Legge, Kennedy, Lloyd, Murphy, & Fisher, 2011). Secondly, relatively high feral cat activity has been reported in areas with a natural- or disturbance-created open understorey (Hohnen et al., 2016; McGregor, Legge, Jones, & Johnson, 2014). For example, feral cats have been recorded moving rapidly towards recently burnt areas (McGregor, Legge, Jones, & Johnson, 2016) and have increased activity following fires (Leahy et al., 2016). This behaviour is likely due to greater hunting efficiency of feral cats in areas with a more open understorey, compared to dense grassy or rugged habitats in northern Australia (McGregor, Legge, Jones, & Johnson, 2015).

This research indicates that altered fire regimes and overgrazing by introduced herbivores simplify habitat structural complexity in northern Australia and that feral cats are attracted to these disturbed and open habitats, having greater hunting efficiency in these areas. However, it remains unclear whether the initial depletion of resources due to disturbance, or a subsequent increase in predation pressure by feral cats specifically, is the predominant driver of mammal decline in northern Australia. Part of this confusion is because we lack

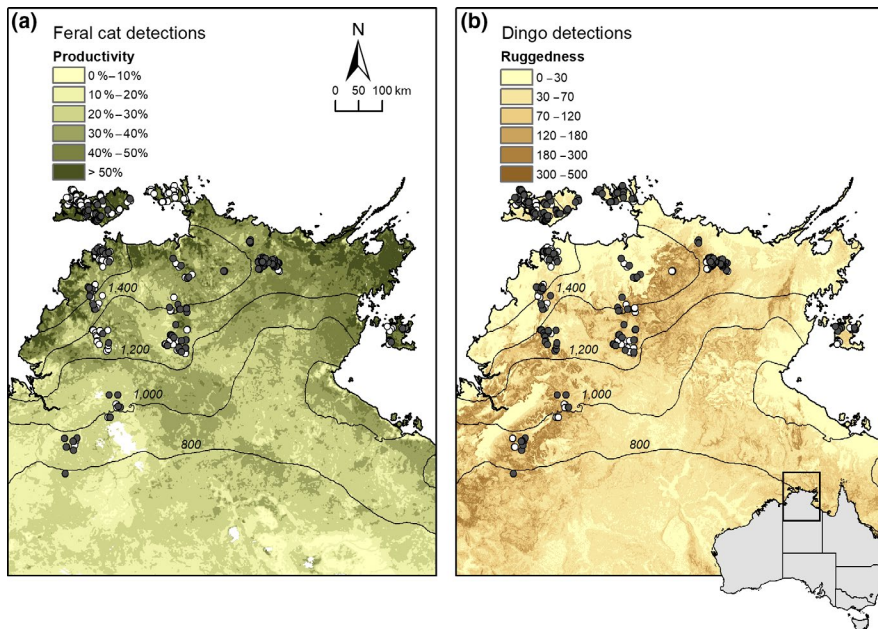


FIGURE 1 Location of study sites across monsoonal areas of the Northern Territory, with respect to regional (a) productivity (green vegetation density cover averaged over 1.6 km from 2005 to 2014) and (b) ruggedness (terrain ruggedness index averaged over 3.2 km). Dark circles indicate sites where (a) feral cats or (b) dingoes were detected. White circles indicate sites where the respective species were not detected. Black lines represent 200-mm interval rainfall isohyets. Inset—the location of the study area relative to Australia

an understanding of the drivers of the distribution and abundance of feral cats at a landscape scale. Relatively high feral cat activity has been observed at localized scales in recently burnt areas and areas with an open understorey (e.g., McGregor, Legge, et al., 2016). However, we do not know what broader impact a local increase in cat activity and predation pressure has on mammal populations. Thus, a better understanding of the distribution of mammalian predators in northern Australia is a necessary first step in managing mammal declines.

A major barrier to landscape-scale feral cat research in northern Australia is the regionally low detectability of feral cats (Stokeld et al., 2016) and the consequent effort required to achieve adequate detections to model feral cat occurrence or population density. The only study to successfully model feral cat occurrence in northern Australia found that feral cats were less likely to occur in rocky, rugged habitats (Hohnen et al., 2016). However, the study was specific to two localized areas of northwestern Australia, capturing just a fraction of the environmental variability that occurs across northern Australia more broadly. Conversely, recent modelling of geographic variation in the abundance of feral cats at a national scale lacks the resolution to identify variation in abundance within northern Australia and includes only a small set of explanatory factors (Legge et al., 2017).

Compared to feral cats, there has been far less consideration of the role of dingoes (*Canis familiaris* [dingo]), in northern Australia's mammal decline. In Australia, there is a long-standing debate as to whether dingoes, a top predator present in Australia for ca. 4,000 years, limit feral cat populations (e.g., Allen, Allen, & Leung, 2015; Hayward & Marlow, 2014; Nimmo, Watson, Forsyth, & Bradshaw, 2015), including in northern Australia (Allen, Allen, Engeman, & Leung, 2013; Kennedy, Phillips, Legge, Murphy, & Faulkner, 2012; Leo, Reading, Gordon, & Letnic, 2019). The presence of healthy dingo populations might provide a net benefit to CWR mammals susceptible to feral cat predation. Conversely, there has been little emphasis on the potentially negative impacts dingoes might have on CWR mammal populations, despite

evidence of increased dingo activity following fire events (Leahy et al., 2016), and in open habitats (Marrant, Johnson, Butler, & Congdon, 2017). A recent study from northern Australia (Stokeld et al., 2018) showed that CWR mammals may form a larger proportion of dingo diets than previously recognized. Furthermore, there is evidence that dingoes have the capacity to suppress populations of threatened CWR mammal species (Allen & Leung, 2012), including the northern quoll (*Dasyurus hallucatus*), a native small predator (Cremona, Crowther, & Webb, 2017; Jolly, Kelly, Gillespie, Phillips, & Webb, 2018). In the context of landscape-scale changes to habitat structural complexity in northern Australia, CWR mammals may now be more susceptible to, and have a lower capacity to withstand, predation pressure from dingoes than they were historically (Allen et al., 2018). Thus, a better understanding of the distribution of dingoes at a landscape scale is also required to assess the role of dingoes in the decline of CWR mammals in northern Australia (Allen, 2011).

We modelled feral cat and dingo site occurrence, accounting for imperfect detection, to provide the first broad-scale assessment of their distributional patterns and co-occurrence within monsoonal Australia. We used a hypothesis-driven approach to determine the most influential environmental and disturbance-related predictors of feral cat and dingo occurrence. Our aim was to evaluate the respective contribution of feral cats and dingoes in the current pattern of mammal decline in northern Australia to inform regional conservation management efforts.

2 | METHODS

2.1 | Study region

We focused on the northernmost section of the Northern Territory, Australia, commonly referred to as the “Top End”

(Figure 1). The region is part of the world's largest remaining expanse of tropical savanna woodland (Bradshaw, 2012), dominated by eucalypts (*Eucalyptus* and *Corymbia* spp.) with pockets of monsoon rainforest, sandstone heath, floodplain, wetland and riparian forest communities (Bowman et al., 2010; Williams et al., 1996). The region is characterized by a monsoonal wet-dry tropical climate, with mean annual rainfall ranging from 700 mm at the southern edge to 1,900 mm in the northern coastal areas; majority of rainfall (>90%) occurs during the wet season (December–April).

We surveyed 376 sites throughout the study region (ca. 370,000 km²), covering all major vegetation types (except floodplains), and a range of land tenures, including National Parks (Kakadu, Litchfield, Nitmiluk, Garig Gunak Barlu and Judburra/Gregory), Indigenous Protected Areas (Groote Eylandt, Wardaman, Warddeken and Djelk), privately owned conservation reserves (Fish River Station) and Indigenous freehold land (Melville Island and Bathurst Island). Note that we did not sample areas of pastoral lands in which dingoes are managed to reduce their abundance. No known targeted management of feral cats or dingoes has occurred in the vicinity of our survey sites.

2.2 | Data collection

2.2.1 | Camera-trap survey

We used camera traps to collect detection/non-detection records of feral cats and dingoes at each site. All sites were surveyed once between August 2013 and June 2016, with an average survey length of 50 nights (range: 26–80 nights). Average distance between sites was 2.5 km (minimum distance between sites 0.1–17.6 km; maximum distance between sites 771.1 km). Five motion-sensor cameras were deployed at each site in a diamond configuration, with a single camera in the centre and four cameras placed between 30 and 50 m from the centre camera (see Gillespie et al., 2015 for further details). We deployed infrared and white-flash cameras (Reconyx HC550, HC600 or PC850, Holmen), with a mixture of all camera models at each site. Cameras were secured to a tree or other solid structure, 50–70 cm above ground. As this survey was part of a broader biodiversity study, each camera was deployed with a bait station. Bait stations were constructed using 80 mm length PVC pipe with ventilated end caps and contained a standard small mammal bait mix of peanut butter, oats and honey, not purposefully designed to attract dingoes or cats. Bait stations were secured to metal stakes 30 cm above ground, 1.5–3 m from the camera, with Coopex Residual Insecticide[®] powder (Bayer AG) at the base to deter ants. Understorey vegetation directly in front of the camera was removed to maximize animal detections and minimize false triggers. Cameras were programmed to take three successive photographs following each trigger, with a one-second interval between photographs. Cameras were run continuously, and each image was date- and time-stamped.

2.2.2 | Predictor variables

To model spatial patterns of site occupancy by feral cats and dingoes, we used predictor variables that relate to plausible competing hypotheses of predator occupancy in northern Australia, including prey abundance, fire, productivity, anthropogenic disturbance, ruggedness, large introduced herbivore activity and feral pig presence (see Appendix S1, Table S1.1 for a list of hypotheses and Table S2 for complete suite of predictor variables used for analyses). Where possible, satellite-derived predictor variables (indices of fire, ruggedness, productivity and anthropogenic disturbance) were extracted at multiple spatial scales (i.e., calculated over various neighbourhood radii), as the scale at which these variables may influence feral cat and dingo occupancy is not well understood.

We did not use the abundance of CWR mammals as a predictor covariate for either feral cat or dingo occupancy. Despite evidence that feral cats and dingoes predate on CWR mammals (Stokeld et al., 2018; Woinarski, 2015), drivers of the abundance of CWR mammals are currently uncertain; therefore, modelling the influence of CWR mammal abundance on feral cat and dingo occurrence would be difficult to interpret (unable to distinguish between cause and effect). We intend to investigate this issue in future work using a similar dataset.

2.3 | Data analysis

All analyses were conducted in R (R Core Team, 2017). Prior to modelling, we followed the protocol for data exploration provided by Zuur, Ieno, and Elphick (2010). Explanatory variables were standardized prior to analysis.

We used single-species occupancy models that explicitly account for imperfect detection (MacKenzie et al., 2002) to investigate site occupancy by feral cats and dingoes. We generated detection histories for both feral cats and dingoes for each study site across the entire survey period (one trap night was 24 hr, i.e., 12:00 p.m. to 11:59 a.m.). We collapsed detection histories from the five camera stations at each site to form one detection history per site for each species. We modelled the influence of predictor variables on detectability (p ; probability a species was detected at a site on a given night, if present) and occupancy (Ψ ; probability a species was present at a site) of both species using the R package “unmarked” (Fiske & Chandler, 2011).

To account for potential survey biases, we modelled the influence of the time of year of each survey (Julian day; taken as the midpoint of the survey for each site due to differing survey lengths) and the number of cameras operating at each site (survey effort; as not all cameras were operational in a given night) on feral cats and dingo detectability. To investigate potential variation in feral cat and dingo occurrence on offshore islands versus mainland sites, we modelled feral cat and dingo occupancy from the full dataset (376 sites), mainland sites only (246 sites) and island sites only (130 sites). Feral pig detection and introduced herbivore activity were not included in candidate model sets

for the island-only dataset as histograms of these variables showed little variation in values (primarily because Groote Eylandt has no introduced herbivores and pigs, and no introduced herbivore activity was recorded from the Bathurst Island sites).

2.3.1 | Single-species occupancy models

To test hypotheses of feral cat and dingo occupancy, we used a three-step modelling approach, which accommodated the large number of predictor variables and subsequent large candidate model set. Firstly, we selected only a limited number of predictor variables, with each corresponding to a particular hypothesis (i.e., prey abundance, fire, productivity, anthropogenic disturbance, ruggedness, large introduced herbivore activity and feral pig presence; see Appendix S1, Table S1.2). To do this, we used Akaike's information criterion (AIC) to rank the suite of predictor variables that corresponded to a given hypothesis (Burnham & Anderson, 2002) and to determine the strongest predictor variable for each hypothesis. The model with the lowest AIC by ≥ 2 was used to test hypotheses of feral cat and dingo occupancy. These final predictor variables were as follows: introduced herbivore activity index, feral pig presence, macropod activity index, average proportion of area burnt over a 10-year time period within a 3.2 km radius, average terrain ruggedness index within a 3.2 km radius, anthropogenic disturbance index averaged over a 10 km radius, average green vegetation density within a 1.6 km radius and island versus mainland sites.

Secondly, we determined which predictor variables (including the two variables specific to detectability—survey effort and Julian day—and the eight variables relevant to leading hypotheses of occupancy) best explained the detectability of each species. This process involved running all possible combinations of the 10 predictor variables on species detectability, while constraining occupancy to a saturated model that included the above-mentioned eight predictor variables. We again used AIC to select the most parsimonious model in the candidate set, and the model with the lowest AIC by ≥ 2 was deemed the best model of feral cat and dingo detectability.

Lastly, we used a combination of univariate and multivariate models to test the final suite of predictor variables relevant to hypotheses of feral cat and dingo occupancy; detectability was held constant using the predictor variables that were identified as significant for each species. We assessed model fit of the top-ranked model with a goodness-of-fit test based on parametric bootstrapping and Pearson's chi-square statistic (must be >0.05). This method repeatedly simulates datasets based on a fitted model and then evaluates the probability that the observed history of outcomes was generated by the model (MacKenzie & Bailey, 2004).

2.3.2 | Two-species occupancy models

We used two-species occupancy models (Richmond, Hines, & Beissinger, 2010), to investigate the potential influence of dingo

occupancy on feral cat detectability and feral cat occupancy. Two-species occupancy models test for evidence of competitive exclusion by modelling the probability of occupancy for a subordinate species (feral cats) conditional upon the presence of a dominant species (dingoes). From the single-species occupancy models, we used the best predictors of feral cat and dingo detectability and occupancy to develop a set of candidate models for testing whether: (a) detection of feral cats was conditional on the detection or occurrence of dingoes; (b) occurrence of feral cats was conditional on the presence of dingoes; and (c) co-occurrence of both species was influenced by predictors of dingo occupancy and other predictor variables hypothesized to interact with dingo occupancy (indices of fire and productivity). We fitted two-species occupancy models using the "wqid" package (Meredith, 2019), with the single-season two-species occupancy estimation function "occ2sps." Models were ranked according to AIC, and the model with the lowest AIC by ≥ 2 units was deemed the best model.

3 | RESULTS

There were 291 feral cat and 925 dingo detections from 83,357 trap nights across all sites. The naïve occupancy (i.e., proportion of sites the species was detected) of feral cats and dingoes was 33.2% and 52.9%, respectively (Figure 1).

3.1 | Single-species models: feral cats

The best model of feral cat occupancy from those considered included the interaction between proportion of area burnt and green vegetation density (standardized beta coefficient: 1.98; Table 1). Cat occupancy decreased with increasing green vegetation density; however, the magnitude of this effect diminished when there was a greater proportion of area burnt (proportion of area burnt increased feral cat occupancy; Figure 2a). The best model of feral cat occupancy and detectability predicted that the probability of site occupancy was 43.9%. This model also predicted that over 50 nights (mean survey length), there was a 79% probability of detecting a feral cat, if present. Anthropogenic disturbance, green vegetation density and the proportion of area burnt were significant terms to include for feral cat detectability and were all included in the final suite of hypothesis testing models. The detectability of feral cats increased with indices of anthropogenic disturbance (0.56), but decreased with proportion of area burnt (-0.40) and green vegetation density (-1.21).

The best predictors of feral cat occupancy and detectability were consistent when modelling occupancy from all sites and with mainland sites only (Table 1). When modelling feral cat occupancy from island sites only, the proportion of area burnt was the only significant predictor (Table 1); cat occupancy again increased with the proportion of area burnt. Anthropogenic disturbance and proportion of area burnt remained significant terms for feral cat detectability at

TABLE 1 Model selection results for predicting feral cat and dingo occupancy. Only single-species occupancy models that significantly improved model fit are presented (lower AIC by ≥ 2 AIC units from the null model) for (a) all sites (376 sites), (b) mainland-only sites (246 sites) and (c) island-only sites (130 sites)

Hypothesis (for occupancy)	Occupancy component of the model	Δ AIC	w_i
Feral cat occupancy			
(a) All sites			
Fire \times Productivity	Proportion burnt \times Green vegetation density	0	0.91
Ruggedness	Ruggedness	5.6	0.06
Productivity	Green vegetation density	8.9	0.01
Null		11	<0.01
(b) Mainland sites only			
Fire \times Productivity	Proportion burnt \times Green vegetation density	0	0.92
Ruggedness	Ruggedness	6.8	0.03
Null		8.8	0.01
(c) Island sites only			
Fire	Proportion burnt	0	0.84
Anthropogenic disturbance	Anthropogenic disturbance	4	0.11
Null		8.7	0.01
Dingo occupancy			
(a) All sites			
Ruggedness	Ruggedness	0	0.92
Introduced herbivores	Introduced herbivore activity index	5.9	0.05
Fire + Introduced herbivores	Proportion burnt + Introduced herbivore activity index	7.8	0.02
Null		12.3	<0.01
(b) Mainland sites only			
Ruggedness	Ruggedness	0	0.90
Introduced herbivores	Introduced herbivore activity index	4.5	0.10
Fire + Introduced herbivores	Proportion burnt + Introduced herbivore activity index	11.5	0.00
Feral pigs	Feral pig presence	17.8	0.00
Null		20	0.00
(c) Island sites only			
Fire	Proportion burnt	0	0.72
Null		4.6	0.07

Note: w_i , Akaike's weight; Δ AIC, difference between the model's AIC (Akaike's information criterion) value and that of the top-ranking model. Bold text indicates most supported models (Δ AIC ≤ 2). See Appendix S1 for complete description of predictor variables and full model selection results table.

island sites (detectability increased with disturbance and decreased with proportion of area burnt), but green vegetation density was no longer a significant term.

3.2 | Single-species models: Dingoes

The best model of dingo occupancy contained just one variable as a predictor of dingo occupancy, terrain ruggedness (Table 1), with dingo occupancy decreasing as ruggedness increased (-0.89 ; Figure 2b). The best model of dingo occupancy and detectability predicted that the probability of site occupancy by dingoes was 60.4%. This model also predicted that over 50 nights, there was a 96% probability of detecting a dingo, if present. Detectability of dingoes significantly increased with Julian day (0.34), survey effort (0.35), proportion of area burnt (0.41) and introduced herbivore activity (0.29); all variables were included in the final suite of hypothesis testing models.

The best predictors of dingo occupancy and detectability were consistent when modelling occupancy from all study sites and again with mainland sites only (Table 1). However, when modelling dingo occupancy from island sites only, we found the proportion of area burnt was the best predictor of dingo occupancy (Table 1); dingo occupancy decreased as the proportion of area burnt increased. Julian day, survey effort, fire and introduced herbivores remained significant terms for dingo detectability.

3.3 | Two-species models: feral cats and dingoes

Dingo occupancy was not a significant predictor of feral cat detectability or occupancy. This was also true when additional predictor variables were included in the two-species model and when modelling occupancy from mainland sites and island sites only (Table 2). Models that assumed no effect of dingo occupancy on either feral cat detectability or feral cat occupancy received the strongest support (Table 2). Model weight decreased for all combinations of predictor variables when feral cat detectability and feral cat occupancy were conditional on dingo occupancy.

4 | DISCUSSION

Our study provides a unique landscape-scale perspective on patterns of feral cat and dingo occurrence in northern Australia. Two key results emerge from our analyses. Firstly, we found that feral cat occurrence and dingo occurrence were best predicted by different indices of habitat structural complexity (Table 1; Figure 2). Feral cat occurrence declined with increasing productivity (inferred from green vegetation density), but with a less pronounced decline in areas of relatively high fire activity (proportion of area burnt averaged over ten years). In contrast, dingo occurrence declined with greater terrain ruggedness such that dingoes were more prevalent in relatively flat, lowland areas. Secondly, we

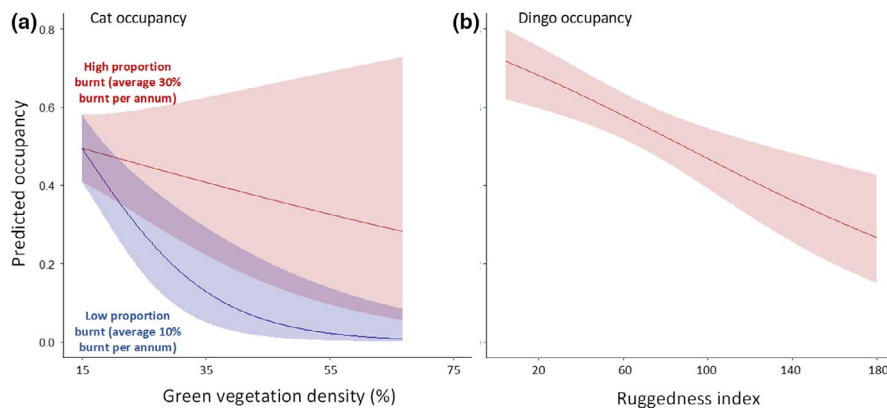


FIGURE 2 Modelled relationships for (a) predicted feral cat occupancy against green vegetation density (as an index of productivity) depending on the proportion of area burnt (within 3.2 km averaged over a 10-year time period; high proportion burnt is red, and low proportion burnt is blue) and (b) predicted dingo occupancy against an index of ruggedness. Lines indicate model predictions, and shaded bands indicate 95% confidence intervals

found no evidence that feral cat occurrence was spatially limited by the occurrence of dingoes (Table 2); instead, we found contrasting patterns of habitat use between the two species. In northern Australia, CWR mammal declines appear to have been less severe in areas of greater habitat structural complexity (i.e., relatively productive and/or rugged areas; Davies et al., 2018; Start et al., 2007). Our findings suggest that low predator presence in these areas may in part explain this pattern. However, in view of the perceived higher abundance of prey in these areas (which could not be directly quantified in this study), the underlying reasons for this low occurrence of cats and dingoes are unclear and highlight an important knowledge gap.

We found the interaction between productivity and fire activity predicted feral cat occurrence better than any single environmental variable (Figure 2a). Within the tropical savannas of northern Australia, high primary productivity tends to correspond with habitat structural complexity (Williams et al., 1996). However, where there is high fire activity, structural complexity deteriorates due to short- and long-term reductions in the density of ground cover and the shrubby mid-storey (Russell-Smith et al., 2012; Williams et al., 1999). We suggest that high fire activity in more productive environments enables feral cats and potentially other predators to access prey (i.e., CWR mammals) which would otherwise be less accessible due to greater structural complexity. Only a minority of our sites had both high productivity (>35% average green vegetation density) and high fire activity (>30% average proportion of area burnt per year, within a 3.2 km radius); thus, although this result is significant it requires further exploration. This finding adds to the growing body of work in northern Australia showing feral cats are more likely to use landscapes with an open understorey, typically due to disturbance (e.g., fire and feral herbivores; Hohnen et al., 2016; McGregor et al., 2014).

Very few studies have investigated spatial patterns of dingo occurrence in northern Australia. Across our study region, dingo occurrence was highest in areas of low ruggedness, highlighting that habitat structural complexity is also a potential driver of dingo occurrence in northern Australia (Figure 2b). The only previous study of habitat use by dingoes within our study region found that dingoes use most available habitat types, with strong

seasonal variation in habitat use due to prey availability (Corbett, 1995). However, that study was relatively localized with all sites in lowland habitats. Other studies throughout northern Australia more broadly have found dingo activity is greatest in open and simplified habitats (Marrant, Johnson, et al., 2017), with dingoes only occasionally utilizing rugged areas (Thomson, 1992). Dingoes are opportunistic hunters that typically chase, rather than ambush, their prey (Corbett, 1995; Marrant, Wurster, Johnson, Butler, & Congdon, 2017). Thus, we suggest areas of low topographic complexity provide better hunting grounds for dingoes, relative to the rugged regions of northern Australia.

We found no evidence that feral cat occurrence is spatially limited by the occurrence of dingoes (Table 2). Different predictors of site occurrence for feral cats and dingoes offer an alternative explanation as to why there is low spatial overlap between feral cats and dingoes at a local scale in northern Australia (Brook, 2013). Where other studies suggest dingoes have a top-down influence on feral cats and ultimately suppress feral cat populations (Brook, Johnson, & Ritchie, 2012), it is also plausible that feral cats simply exploit different habitats and resources than that of dingoes (Edwards, Preu, Crealy, & Shakeshaft, 2002; Fancourt, Cremasco, Wilson, & Gentle, 2019; Wang & Fisher, 2012). Therefore, low spatial overlap at a local scale may reflect different patterns of habitat use rather than spatial avoidance of dingoes by feral cats. Our study does not rule out the potential for temporal avoidance of dingoes by feral cats. Some studies have found top predators and mesopredators often utilize similar habitats; however, mesopredators avoid top predators at a local scale, rather than avoiding the area altogether (Broekhuis, Cozzi, Valeix, McNutt, & Macdonald, 2013; Fancourt, 2016). Broekhuis et al. (2013) suggest mesopredators may employ a more reactive response to top predator avoidance rather than a predictive response (i.e., complete spatial avoidance). Further studies that employ a similar landscape-scale approach as that employed here are required to better understand the subtleties of the relationship, if any, between feral cats and dingoes in northern Australia. Based on the existing body of work, there is insufficient evidence to suggest dingoes are limiting the distribution, or constraining the habitat use, of feral cats in northern Australia (Allen et al., 2015).

TABLE 2 Model selection results for the top-three performing two-species occupancy models. Models examine interactions between feral cat and dingo occupancy, for (a) all sites (376 sites), (b) mainland-only sites (246 sites) and (c) island-only sites (130 sites)

Hypothesis (for occupancy)	Occupancy component of the model	ΔAIC	w
(a) All sites			
<ul style="list-style-type: none"> Dingo occupancy varies with "Ruggedness" Cat occupancy independent of dingo occupancy and varies with "Fire * Productivity" 	psiD ~ Ruggedness, psiCd ~ Proportion burnt \times Green vegetation density	0.0	0.93
<ul style="list-style-type: none"> Dingo occupancy varies with "Ruggedness" Cat occupancy dependent on dingo occupancy and varies with "Fire * Productivity" 	psiD ~ Ruggedness, psiCd ~ Proportion burnt \times Green vegetation density, psiCD ~ Proportion burnt \times Green vegetation density	5.6	0.06
<ul style="list-style-type: none"> Dingo occupancy varies with "Ruggedness" Cat occupancy dependent on dingo occupancy and varies with "Ruggedness" 	psiD ~ Ruggedness, psiCd ~ Ruggedness, psiCD ~ Ruggedness	8.5	0.01
(b) Mainland sites only			
<ul style="list-style-type: none"> Dingo occupancy varies with "Ruggedness" Cat occupancy independent of dingo occupancy varies with "Fire * Productivity" 	psiD ~ Ruggedness, psiCd ~ Proportion burnt \times Green vegetation density	0.0	0.92
<ul style="list-style-type: none"> Dingo occupancy varies with "Ruggedness" Cat occupancy dependent on dingo occupancy and varies with "Fire * Productivity" 	psiD ~ Ruggedness, psiCd ~ Proportion burnt \times Green vegetation density, psiCD ~ Proportion burnt \times Green vegetation density	6.5	0.03
<ul style="list-style-type: none"> Dingo occupancy varies with "Ruggedness" Cat occupancy dependent on dingo occupancy and varies with "Ruggedness" 	psiD ~ Ruggedness, psiCd ~ Ruggedness, psiCD ~ Ruggedness	6.9	0.03
(c) Island sites only			
<ul style="list-style-type: none"> Dingo occupancy varies with "Fire" Cat occupancy independent of dingo occupancy varies with "Fire" 	psiD ~ Proportion burnt, psiCd ~ Proportion burnt	0.0	0.65
<ul style="list-style-type: none"> Dingo occupancy varies with "Fire" Cat occupancy dependent on dingo occupancy and varies with "Fire" 	psiD ~ Proportion burnt, psiCd ~ Proportion burnt, psiCD ~ Proportion burnt	2.8	0.16
<ul style="list-style-type: none"> Dingo occupancy varies with "Fire" Cat occupancy dependent on dingo occupancy and varies with "Ruggedness" 	psiD ~ Proportion burnt, psiCd ~ Ruggedness, psiCD ~ Ruggedness	4.7	0.06

Note: pD, dingo detectability; psiD, dingo occupancy; pC, cat detectability; rCd, cat detectability with dingoes absent; rCD, cat detectability with dingoes present; psiCd, cat occupancy with dingoes absent; psiCD, cat occupancy with dingoes present; w_i , Akaike's weight; ΔAIC , difference between the model's AIC (Akaike's information criterion) value and that of the top-ranking model. Bold text indicates the most supported model ($\Delta AIC \leq 2$). See Appendix S1 for complete description of variables and full model selection results table.

4.1 | Implications for biodiversity conservation in northern Australia

The low occurrence of feral cats and dingoes in structurally complex habitats offers new insights into drivers of CWR mammal decline in northern Australia. Firstly, our findings are consistent with the hypothesis that CWR mammals may be persisting in productive areas with greater habitat structural complexity due to relatively low predation pressure by feral cats (Legge et al., 2019; McGregor, Cliff, et al., 2016). However, our analysis also indicates that the persistence of mammals in rugged areas in parts of northern Australia (Start et al., 2007) may be due to the lower occurrence of dingoes in these habitats. Secondly, despite both predators being regarded as opportunistic generalist carnivores (Corbett, 1995; Marrant, Wurster, et al., 2017), this study suggests hunting success (or prey availability) may

be a stronger driver of feral cat and dingo occurrence in northern Australia than is prey abundance. This finding is supported by other research that shows predators are more likely to hunt in areas where they have a higher rate of success (therefore greater prey availability) than in areas where prey abundance is greatest (Kauffman et al., 2007; Pakpien et al., 2017). Thus, although feral cat and dingo abundance might be influenced by local prey abundance (e.g., Molsher, Newsome, & Dickman, 1999; Pavey, Eldridge, & Heywood, 2008), predator distribution and habitat use may be more strongly driven by ease of access to prey, at least in northern Australia. In this study, we were unable to model the influence of CWR mammal abundance on either feral cat or dingo occupancy. However, with this new understanding of the spatial patterns of feral cats and dingoes in northern Australia, we intend to model their respective influence on the distribution of CWR mammals using a similar dataset.

Ours is the first study to detail patterns of feral cat and dingo occurrence at the landscape scale in northern Australia, an area where there has been a severe decline in native mammal fauna. This work has significantly advanced our understanding of the spatial patterns of two key mammalian predators, linking both feral cat and dingo occupancy to habitat structural complexity in northern Australia. This study provides the first landscape-scale evidence of a mechanistic link between the observed patterns of CWR mammal decline with changes to habitat structure complexity in northern Australia, and mammalian predator occupancy. Thus, we have progressed current understanding of the respective roles of these predators in shaping contemporary patterns of mammal diversity. To continue to resolve the drivers of mammal decline, we now require (a) a more detailed understanding of contemporary patterns of CWR mammal diversity in northern Australia and (b) a clearer understanding of the functional relationships between feral cats and prey population dynamics, and productivity and disturbance regimes. Our study highlights the importance of maintaining and potentially expanding structurally complex habitats to ameliorate predator impacts on CWR mammals. This can be achieved through improved fire and feral herbivore management (Legge et al., 2019) at both a landscape scale (e.g., in productive environments that are currently acting as refugia for a number of declining species, including the Tiwi Islands; Davies et al., 2018) and local management scale (e.g., in productive hotspots within conservation reserves). This approach is likely to be a more successful management option than lethal predator control.

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DATA AVAILABILITY STATEMENT

The datasets used for feral cat and dingo occupancy analysis are available as Data S1. For access to additional data presented in this study, please contact Graeme Gillespie from the Northern Territory Government, Department of Environment and Natural Resources (Graeme.Gillespie@nt.gov.au).

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BIOSKETCH

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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