A Hollow Argument: Understory Vegetation and Disturbance Determine Abundance of Hollow-Dependent Mammals in an Australian Tropical Savanna

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Native mammals are suffering widespread and ongoing population declines across northern Australia. These declines are likely driven by multiple, interacting factors including altered fire regimes, predation by feral cats, and grazing by feral herbivores. In addition, the loss of tree hollows due to frequent, intense fires may also be contributing to the decline of hollow-dependent mammals. We currently have little understanding of how the availability of tree hollows influences populations of hollow-dependent mammals in northern Australian savannas. Here, we test the hypothesis that the abundance of hollow-dependent mammals is higher in areas with a greater availability of tree hollows. We used camera-trap data from 82 sites across the savannas of Melville Island, the largest island in monsoonal northern Australia. Royle–Nichols abundance-induced heterogeneity models were used to investigate the biophysical correlates of the abundance of three threatened mammals: northern brushtail possum (*Trichosurus vulpecula arnhemensis*), black-footed tree-rat (*Mesembriomys gouldii*), and brush-tailed rabbit-rat (*Conilurus penicillatus*). Our analyses included two variables that reflect the availability of tree hollows: the density of tree hollows, estimated from the ground, and the density of large eucalypt trees (*Eucalyptus* and *Corymbia* spp.). We found no evidence that the abundance of the three hollow-dependent mammals is positively associated with the availability of tree hollows on Melville Island. Despite their reliance on hollow-bearing trees for denning, the abundance of these mammals appears to be more strongly associated with other factors, such as the characteristics of the understory (i.e., shrub density), which affords protection from predators (including feral cats) and access to food resources. Future conservation management should aim to maintain a dense, diverse understory by managing fire and feral herbivores to facilitate the persistence of hollow-dependent mammals across northern Australia.

Keywords: cavity-bearing trees, eucalypts, fire management, land management, mammal decline, marsupials, tropical savanna, rodents

INTRODUCTION

Australia has lost around 10% of its native terrestrial mammal species since the arrival of Europeans almost 250 years ago (Short and Hide, 2012; Woinarski et al., 2015). Introduced predators and/or habitat modification have been implicated in the majority of mammal declines and extinctions in Australia (Woinarski et al., 2014, 2019). Mammal declines and extinctions have been pervasive and severe among species with a body size in the so-called "critical weight range" (35–5,500 g; Cardillo and Bromham, 2001; Johnson and Isaac, 2009). Whereas most mammal extinctions occurred in central and southern Australia before the mid-20th Century, there are now severe declines occurring across the vast, uncleared savanna landscapes of northern Australia (Woinarski et al., 2010, 2011). Drivers of these declines have been difficult to identify, despite being one of Australia's most pressing biodiversity conservation challenges. However, a recent conceptual model postulates that the decline of native mammals across northern Australia reflects the interaction between habitat degradation (through overgrazing by feral herbivores and livestock and altered fire regimes) and predation processes (Stobo-Wilson et al., 2020a).

A disproportionate number of mammals in northern Australian savannas that have experienced severe declines are arboreal and semi-arboreal species that are reliant on tree-hollows for denning (Taylor et al., 2003; Woinarski et al., 2011). Once common across the savannas, hollow-dependent mammals have typically contracted to the higher rainfall, higher productivity parts of their ranges (Woinarski et al., 2014; von Takach et al., 2020), where large trees and hollows are most abundant (Woolley et al., 2018). Existing studies have noted the importance of eucalypts as den trees for northern Australian arboreal rodents and marsupials (Griffiths et al., 2001; Firth, 2003; Hohnen et al., 2015; Penton et al., 2020b; Stobo-Wilson et al., 2021). Stobo-Wilson et al. (2021) demonstrated den tree selection by the savanna glider (*Petaurus ariel*) differed based on hollow availability, highlighting the influence of hollow limitation in lower rainfall areas of the tropical savannas.

It has been suggested that an increase in the frequency of high-intensity fires in recent decades has reduced the abundance of large hollow-bearing trees in northern Australia's savannas (Woolley et al., 2018), which likely has had a negative impact on hollow-dependent mammals (Firth et al., 2010; Woinarski et al., 2011). Studies from temperate forests in Australia and overseas show a loss in hollow-bearing trees is typically associated with a decline in hollow-dependent fauna (Lindenmayer and Cunningham, 1997; Aitken and Martin, 2008; Cockle et al., 2010). As such, there may be a direct link between the decline of hollow-dependent mammals in northern Australian savannas and fire-driven loss of tree hollows.

To investigate whether the availability of tree hollows limits populations of hollow-dependent mammals in a high-rainfall tropical savanna, we analyzed camera-trap data on Melville Island, the largest island in monsoonal northern Australia (**Figure 1**). We hypothesized that the availability of tree hollows would be strongly correlated with the abundance of hollow-dependent mammals on Melville Island, while the attributes of the understory, such as shrub density, would be of secondary importance.
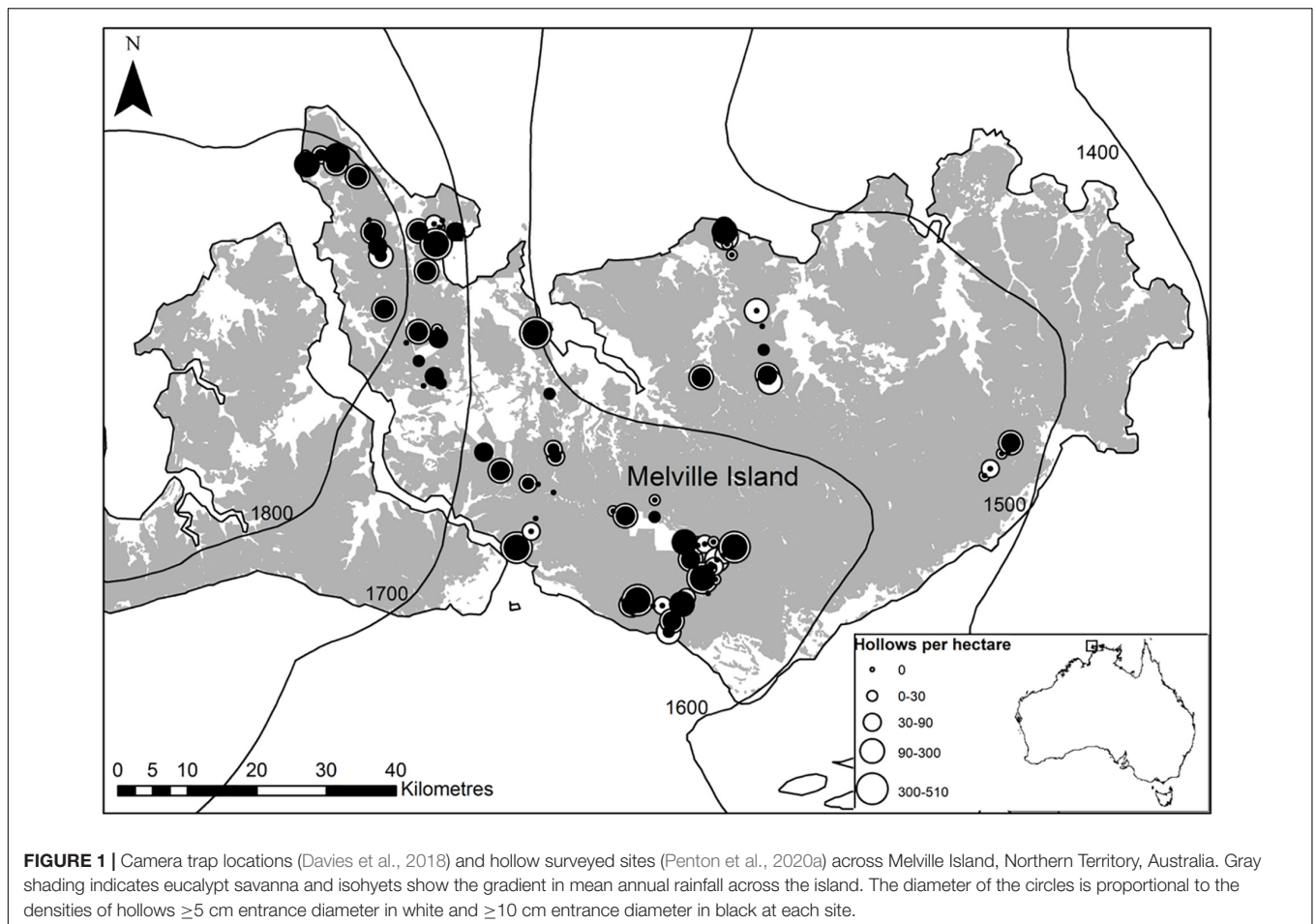
MATERIALS AND METHODS

Study Site

Melville Island is situated approximately 25 km off the central coast of northern Australia, and is Australia's second-largest island (5,786 km^2) (**Figure 1**). Melville Island is the larger of the two main Tiwi Islands, a critical refuge for numerous mammal species that are in severe decline on the northern Australian mainland. However, recent evidence shows that mammals have declined on Melville Island over the last two decades (Davies et al., 2018). Although the declines have not progressed to the same extent as the mainland, the same processes are likely impacting the island populations (Stobo-Wilson et al., 2020a).

Melville Island experiences a tropical monsoonal climate, with over 90% of rainfall occurring in the wet season (Australian Bureau of Meteorology, 2020a). There is a substantial gradient in mean annual rainfall across the island, from 1,400 mm in the east to 2,000 mm in the north-west. Tropical savanna, dominated by tall eucalypts (predominantly *Eucalyptus miniata*, *Eucalyptus tetrodonta*, and *Corymbia nesophila*), covers 75% of the island (Woinarski et al., 2003). The understory is predominantly grassy, and shrub density is highly variable. Due to the high density of large trees, Melville Island generally supports a higher tree hollow densities than the adjacent mainland (Woolley et al., 2018; Penton et al., 2020a). Although hollow densities increase with mean annual rainfall across Melville Island, there is still substantial localized variability, driven by disturbance, such as tropical cyclones, fire, termite activity (Woolley et al., 2018). These forms of disturbance are particularly important drivers of hollow availability on Melville Island because the region is frequently exposed to severe tropical cyclones (Cook, 2001; Cook and Goyens, 2008), experiences very high fire frequencies (Richards et al., 2012), and has particularly high abundance and species richness of termites (Abensperg-Traun and Steven, 1997).

Study Species

We focused on three hollow-dependent, semi-arboreal mammals that once occurred across vast areas of northern Australia at the time of European arrival but are now in various stages of decline (Woinarski et al., 2011, 2014). All three are endemic to the tropical savannas. The northern brushtail possum (*Trichosurus vulpecula arnhemensis*) has declined severely (Stobo-Wilson et al., 2019), and remains abundant only in the highest-rainfall parts of its former range (von Takach et al., 2020), including the Tiwi Islands (Davies et al., 2018, 2021). The black-footed tree-rat (*Mesembriomys gouldii*) is one of Australia's largest rodents and has declined severely in both the Kimberley and mainland Northern Territory (Firth et al., 2010; von Takach et al., 2020), while the Melville Island subspecies (*M. g. melvillensis*) has also shown considerable decline (Davies et al., 2018). Finally, the brush-tailed rabbit-rat (*Conilurus penicillatus*) has experienced a very severe decline (Firth et al., 2010), and the Tiwi Islands subspecies (*C. p. melibius*) has displayed the same rapid pattern

FIGURE 1 | Camera trap locations (Davies et al., 2018) and hollow surveyed sites (Penton et al., 2020a) across Melville Island, Northern Territory, Australia. Gray shading indicates eucalypt savanna and isohyets show the gradient in mean annual rainfall across the island. The diameter of the circles is proportional to the densities of hollows ≥5 cm entrance diameter in white and ≥10 cm entrance diameter in black at each site.

of decline on Melville Island (Davies et al., 2017). All three species (or subspecies in the case of the northern brushtail possum) are listed as Vulnerable under Australia's Environment Protection and Biodiversity Conservation Act (1999). Both rodents are listed as Vulnerable on the IUCN Red List (Burbidge and Woinarski, 2016; Woinarski and Burbidge, 2016).

Penton et al. (2020b) recently identified that the brush-tailed rabbit-rat, black-footed tree-rat, and northern brushtail possum predominantly den in large hollows (≥10 cm entrance diameter), which are generally found in large eucalypt trees [≥30 cm diameter at breast height (DBH), 1.3 m]. Large hollows are relatively scarce in northern Australia's tropical savannas (estimated as only 10% of all hollows in the landscape), and trees with large hollows are particularly vulnerable to disturbance (Murphy and Legge, 2007; Woolley et al., 2018).

Data Collection of Hollow-Dependent Mammal Abundance

In 2015, camera trap surveys were conducted at 88 sites across the lowland savannas of Melville Island (Davies et al., 2017), which had been selected from previous surveys in 2000–2002 (see Firth et al., 2006a). Davies et al. (2017) selected the subset of sites located within savanna woodland, stratified by fire frequency

and rainfall, separated by a minimum distance of 1 km. Each site was surveyed with five horizontally facing motion-sensor cameras deployed in a square formation around a central camera, with 50 m between the central and outermost cameras. A bait station consisting of peanut butter, oats, and honey was placed 1.5 m from two of the five cameras, whereas the remaining three cameras at each site had a bait station placed 2.5 m from the camera (Gillespie et al., 2015). Vegetation within each camera's field of view was cleared to create a fire break and reduce the chance of false triggers, extending battery life. Of the five cameras deployed at each site, two were HC550 Hyperfire white-flash cameras, whereas the remaining three cameras PC800 Hyperfire Professional infra-red flash cameras (Reconyx, Inc., Holmen, WI, United States). Cameras could be triggered at any time of day and were set to a high sensitivity, with cameras programmed to take three images per trigger, with a 1-s interval between images. The cameras were deployed for at least 35 consecutive days (range 35–53 days).

This dataset has been analyzed previously by Davies et al. (2017, 2018), to investigate environmental correlates of the site-occupancy of mammals on Melville Island. However, due to very high site-occupancy rates for both the black-footed tree-rat and northern brushtail possum (Davies et al., 2018), occurring at most sites across the island, and gregarious

social structure of the brush-tailed rabbit-rat (i.e., strong spatial clustering of populations; Firth et al., 2006b; Penton et al., 2020b), we considered that abundance was a more appropriate response variable (cf., site occupancy) to test our hypothesis. Hence, we used Royle–Nichols abundance-induced heterogeneity models, which assume that heterogeneity in detection frequency is indicative of variability in a species' abundance (Royle and Nichols, 2003).

Tree Hollow Availability and Other Environmental Variables

Davies et al. (2017, 2018) investigated a range of environmental correlates of site-occupancy of the brush-tailed rabbit-rat, black-footed tree-rat, and northern brushtail possum. We used similar environmental variables, but to evaluate the influence of the availability of tree hollows and hollow-bearing trees on the abundance of hollow-dependent mammals, we revisited the mammal survey sites in 2017, 2 years after the original survey, and measured two additional variables: (1) hollow density and (2) density of large eucalypts (which are more likely to contain numerous hollows; Woolley et al., 2018; **Table 1**). Six of the sites surveyed in 2015 could not be resurveyed in 2017 and were excluded from the analysis, leaving 82 sites (**Figure 1**).

At each site, a random central reference point was selected following the plotless "point centered quarter" method (Krebs, 1999). To increase number of points sampled up to 12 trees (alive or dead) with a DBH of ≥ 15 cm closest to the central point, equally represented in each quadrant were selected for hollow surveys, which produced a total sample of 963 trees across 82 sites. The hollows in the selected trees were counted from the ground using binoculars. A hollow was defined as having an entrance diameter of ≥ 5 cm. All ground-based surveys were performed by one individual (CP) and were conducted in good light and weather conditions for optimal visibility (e.g., no rain or mist). A minimum of 2 min was spent surveying each tree for hollows from all available vantage points. We recorded the total number of hollows in two entrance diameter classes (5–10 cm and ≥ 10 cm) for each tree. Due to the high frequency of termitaria blocking hollows <10 cm entrance diameter, we calibrated 5–10 cm hollows before calculating total hollow counts (≥ 5 cm and ≥ 10 cm entrance diameter) using a subset of trees that were double sampled with climbing surveys (Penton et al., 2020a).

We also recorded calculated large eucalypts (dead or alive) ≥ 30 cm DBH at each site from the original tree dataset, which produced a sub-sample of 465 trees across the 82 sites. We calculated hollow and large eucalypt densities using the plotless "point-centered quarter" method where the area around the random point is divided into four quadrants, and the distance to the nearest tree is measured in each quadrant:

$$Estimated \ \mathrm{density} \ \left(ha^{-1}\right) = \frac{4 \ (4 \ (n) - 1)}{\pi \, \Sigma \, (r_{ij}2)}$$

Where n is the number of samples and r_{ij} is the distance (m) from random point i to the closest individual in quarter j (Krebs, 1999; Jamali et al., 2020).

TABLE 1 | Description of the variables used in the analyses to assess the correlates of Melville Island arboreal mammal distribution in 2015.

| Environmental variable	Coding	Measurement
Mean annual rainfall	Continuous, centered, and standardized	Mean annual rainfall (mm per annum) (Australian Bureau of Meteorology, 2020b)
Distance to watercourse	Continuous, centered, and standardized	The distance (m) from each site to the closest watercourse derived from Geoscience Australia DEM SRTM 1 Second Hydrologically Enforced Map
Dingoes	Categorical	Presence/absence of dingoes. If a dingo was recorded once at the site, it was recorded as present
Large feral herbivores	Categorical	Presence/absence of large feral herbivores. If a feral herbivore was recorded once at the site, it was recorded as present. Feral herbivores included water buffalo (*Bubalus bubalis*) and horse (*Equus caballus*)
Feral cat activity	Continuous, centered, and standardized	As an index of feral cat activity. We used the predicted probability of detecting feral cats at each site, derived from spatially explicit generalized linear models (Murphy et al., 2010)
Fire frequency	Continuous, centered, and standardized	The number of times a site had been burned in the previous 5-year period (Lawes et al., 2015) immediately before the faunal survey (2015) from the Northern Australia Fire Information (NAFI) dataset (www.firenorth.org.au)
Coarse woody debris	Continuous, centered, and standardized	A count of the number of logs with a diameter of >5 cm that crossed a 200 m long transect at each site
Shrub density	Continuous, centered, and standardized	A count of the number of shrubs in a 1 m × 100 m quadrat at each site. Shrubs were defined as anything taller than 20 cm but shorter than 1.3 m or taller than 1.3 m with a diameter at breast height of <5 cm. Shrubs with multiple stems were counted as a single individual
Large eucalypt density*	Continuous, centered, and standardized	Plotless PCQ method surveying eucalypts ≥ 30 cm DBH (dead or alive) at each site
Hollow density*	Continuous, centered, and standardized	Plotless PCQ method surveying trees ≥ 15 cm DBH for hollows 5–10 cm and ≥ 10 cm entrance diameter. Hollows 5–10 cm were calibrated before calculating total hollows ≥ 5 cm entrance diameter for the brush-tailed rabbit-rat and ≥ 10 cm entrance diameter for the larger bodied species at each site

*Between the faunal surveys and commencement of tree surveys Melville Island did not experience any major disturbances at the study sites (i.e., tropical cyclones or late dry season high-intensity wildfires). Six sites were burned between 31/07/2016 and 08/08/2016 (NAFI) just after the carbon abatement cut-off date, though this was not a high-intensity burn.

Penton et al. (2020b) found that den tree selection was significantly correlated with the presence of a large hollow (i.e., ≥ 10 cm entrance diameter) in that tree. They found that

the brush-tailed rabbit-rat used tree hollows with an entrance diameter ≥5 cm. Hence, for this species, we calculated hollow density using hollows with an entrance diameter ≥5 cm (Penton et al., 2020b). For the larger-bodied species (black-footed tree-rat and northern brushtail possum), which tend to use larger hollows, we calculated hollow density using only hollows with an entrance diameter ≥10 cm.

Data Analysis

All analyses were undertaken in the statistical program R (R Core Team, 2020). To examine the relationship between the abundance of three hollow-dependent species and our ten environmental variables (**Table 1**), we used Royle–Nichols abundance-induced heterogeneity models (Royle and Nichols, 2003) in the R package "unmarked" (Fiske and Chandler, 2011).
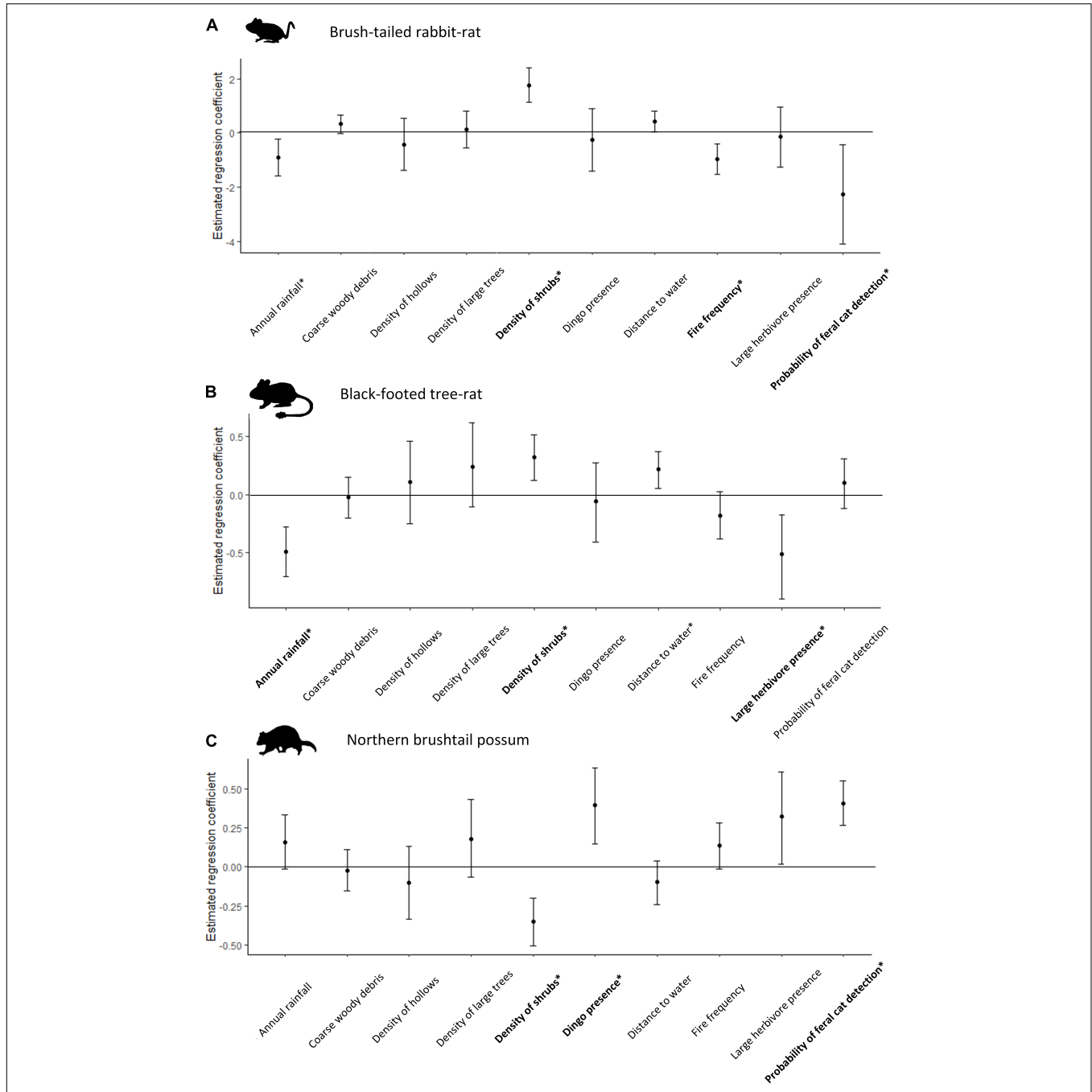
FIGURE 2 | Coefficient estimates for **(A)** brush-tailed rabbit-rat; **(B)** black-footed tree-rat; and **(C)** northern brushtail possum from the global model. Error bars indicate 95% confidence intervals; asterisks indicate where they do not overlap zero, i.e., a statistically significant effect and covariates in bold are for which there was clear evidence of a relationship from the Royle–Nichols models (**Table 2**).

This model assumes that heterogeneity in detection frequency is indicative of variability in a species' abundance by assuming there is a constant probability of detecting each individual, and detections are independent. We created nightly detection histories for each of the three mammal species at each site by dividing the camera surveys into 24-h sampling occasions. Mammal detections were combined for all cameras at each site.

We developed a set of 1,024 candidate models to explain variation in the abundance of each mammal species. This represented all combinations of the ten environmental variables, with no interactions. Models were ranked and evaluated using Akaike's Information Criterion (AIC). All continuous environmental variables were log-transformed, then centered and standardized by deducting the mean and then dividing by twice the standard deviation (Gelman, 2008). We confirmed that there was not excessive collinearity among environmental variables by examining the variance inflation factor (VIF). Following Zuur et al. (2010), we used a conservative VIF threshold of 3; if a variable had VIF > 3 we removed it. We further screened collinearity of variables with known associations (e.g., feral cat activity and fire frequency) with Pearson's correlation coefficient, r, to confirm all variables had a weak or negligible correlation (i.e., $r < 0.45$). We checked for spatial autocorrelation in the residuals of the global model by visually examining variograms of the model residuals and conducted a Moran's I test on the residuals of a linear regression global model with a response variable of total nights the species was recorded at a site in R package "ape" (Paradis and Schliep, 2019); brush-tailed rabbit-rat Moran's $I = 0.08$, $p < 0.001$; black-footed tree-rat Moran's $I = 0.05$, $p = 0.05$; northern brushtail possum Moran's $I = 0.08$, $p = 0.002$ indicating very weak spatial autocorrelation (Moran, 1950).

The abundance of arboreal mammals has been shown to have a "humped response" to hollow availability (Wormington et al., 2002). Thus, we initially considered a quadratic function (i.e., humped relationship) between the abundance of the three mammal species and each of hollow density and large eucalypt density. However, there was no evidence that quadratic relationships were more suitable than linear relationships. We also examined interactions between shrub density and large eucalypt density, the inclusion of the interaction terms did not substantially improve the best models (i.e., AIC reduced by ≥2).

We created a global model, including all ten environmental variables, and plotted the standardized coefficients to evaluate the relative effect sizes of each variable (**Figure 2**). Variables that occurred in all of the well-supported models (ΔAIC ≤ 2; **Table 2**) were considered important environmental variables.

RESULTS

There was significant variability in the density of tree hollows and large eucalypts across Melville Island (**Figure 1** and **Table 3**). Across all sites sampled, the mean density of hollows (entrance diameter ≥5 cm) was 91 ha^{-1} (±12 SE), ranging from 0 to

503 ha^{-1}. Of this, larger hollows (entrance diameter ≥10 cm) contributed 37 ha^{-1} (±7 SE), ranging from 0 to 286 ha^{-1}. Larger hollows were present at only half of the sites surveyed. The mean density of large eucalypts was 66 ha^{-1} (±7 SE), ranging from 0 to 336 (**Table 3**).

We found no evidence that the abundance of the three hollow-dependent mammals was correlated with the density of tree hollows or large eucalypts. Neither hollow density nor large eucalypt density consistently appeared in well-supported models (**Table 2**).

The abundance of all three hollow-dependent mammals was strongly correlated with shrub density. This variable appeared in all well-supported models (**Table 2**). However, the direction of the relationship varied between species, being positive for the brush-tailed rabbit-rat and black-footed tree-rat, which were more abundant at shrubby sites (**Figures 2A,B**), but negative for the northern brushtail possum, which was less abundant at shrubby sites (**Figure 2C**).

Brush-tailed rabbit-rat abundance was strongly negatively correlated with cat activity and fire frequency (**Table 2A** and **Figure 2A**). Black-footed tree-rat abundance was negatively correlated with mean annual rainfall and feral herbivore presence (**Table 2B** and **Figure 2B**). Northern brushtail possum abundance was positively correlated with dingo presence and cat activity (**Table 2C** and **Figure 2C**).

Overall detectability from the best model ranged from 0.86 for the brush-tailed rabbit-rat to 0.99 for both the black-footed tree-rat and northern brushtail possum (**Appendix 1**).

DISCUSSION

We investigated the hypothesis that the availability of tree hollows strongly limits the abundance of hollow-dependent mammals. Despite significant variation in tree hollow availability across Melville Island, we found no evidence to support this hypothesis. We found that factors relating to the quality of the understory (i.e., shrub density, fire frequency, large herbivore presence) and predator assemblages (i.e., predicted cat activity, dingo presence) were stronger correlates of hollow-dependent mammal abundance on Melville Island, than were arboreal habitat features (i.e., hollow density, density of large eucalypts). Our study suggests that a disturbance-driven reduction in the availability of tree hollows has not played a significant role in driving the decline of hollow-dependent mammals on Melville Island, indicating that hollows are not limiting at this region. Rather, patterns of abundance are more strongly influenced by other factors associated with understory habitat quality and ground-based threats (i.e., shrub density and impacts of feral animals). This finding is consistent with recent studies of patterns of the abundance of small mammals across northern Australia more broadly (Davies et al., 2018; Legge et al., 2019; Stobo-Wilson et al., 2019, 2020a).

Although large hollows occur at varying densities across northern Australia's tropical savannas (Woolley et al., 2018), denning behaviors may compensate for variable availability of

TABLE 2 | Model ranking table for the abundance three arboreal mammal species examined on Melville Island 2015: **(A)** brush-tailed rabbit-rat; **(B)** black-footed tree-rat; **(C)** northern brushtail possum.

Response	Mean annual rainfall	Distance to water	Dingo presence/ absence	Feral cat detection probability	Large herbivore presence/ absence	Fire frequency	CWD	Density of shrubs	Density of large eucalypt trees	Hollow density	ΔAIC	wi	Nagelkerke R-squared index
(A) Brush-tailed rabbit-rat Null model; AIC = 624.7, logLik = −308.3	•	•		•		•	•	•			0.0	0.08	0.59
	•			•		•	•	•			0.7	0.13	0.59
	•	•		•		•	•	•		•	1.3	0.17	0.58
				•		•	•	•			1.4	0.20	0.60
	•	•		•		•		•			1.5	0.24	0.57
	•	•	•	•		•	•	•			1.7	0.27	0.58
	•	•		•	•	•	•	•			1.8	0.30	0.60
	•	•		•		•	•	•	•		1.9	0.33	0.60
(B) Black-footed tree-rat Null model = 2134.3, logLik = −1063.1	•	•			•	•		•			0.0	0.03	0.29
	•	•			•			•			0.4	0.06	0.27
	•	•			•			•	•		0.5	0.08	0.29
	•	•			•	•		•	•		0.6	0.11	0.30
	•	•			•			•		•	0.7	0.13	0.29
	•	•		•	•	•		•			1.0	0.15	0.30
	•	•			•			•		•	1.3	0.17	0.30
	•	•			•			•	•	•	1.5	0.18	0.30
	•	•		•	•	•		•	•		1.6	0.20	0.31
	•	•	•		•	•		•			1.7	0.21	0.30
	•	•			•		•	•			1.9	0.22	0.30
	•				•			•			2.0	0.24	0.26
(C) Northern brushtail possum Null model; AIC = 3522.1, logLik = −1757.0	•		•	•	•	•		•			0.00	0.04	0.57
			•	•	•	•		•			0.2	0.07	0.56
			•	•		•		•			0.5	0.10	0.54
	•	•	•	•	•	•		•			0.8	0.12	0.57
	•		•	•	•	•		•	•		1.0	0.15	0.57
		•	•		•	•		•			1.0	0.18	0.56
	•		•	•	•			•			1.0	0.19	0.55

(Continued)

TABLE 2 | (Continued)

Response	Mean annual rainfall	Distance to water	Dingo presence/absence	Feral cat detection probability	Large herbivore presence/absence	Fire frequency	CWD	Density of shrubs	Density of large eucalypt trees	Hollow density	ΔAIC	w_i	Nagelkerke R-squared index
		•						•			1.1	0.21	0.55
			•	•	•			•	•		1.6	0.23	0.56
	•	•	•	•	•	•		•	•		1.6	0.25	0.56
	•	•	•	•	•	•		•	•		1.7	0.26	0.58
	•	•	•	•	•			•	•		1.7	0.26	0.57
	•			•	•			•	•	•	1.7	0.28	0.55
								•			1.8	0.30	0.56
		•	•	•	•	•		•	•		1.8	0.31	0.57
	•	•	•	•	•	•		•			1.9	0.32	0.56
			•			•		•		•	1.9	0.34	0.55
			•	•	•			•	•	•	2.0	0.35	0.57

Royle–Nichols models were ranked according to ΔAIC and w_i is the Akaike weight. The set of candidate models (n = 1,023 models per species) included all combinations of explanatory variables (Table 1), but only models with an ΔAIC ≤ 2 are shown. The AIC and logLik are included for the null model of each species. • is the cumulative AIC weight. Pseudo R-squared is Nagelkerke's (1991) index. The shading indicates variables for which there is clear evidence of a relationship (i.e., the variable appears in all models with ΔAIC ≤ 2).

TABLE 3 | The density of hollows and large eucalypts across the 82 sites surveyed on Melville Island.

Variables	Mean (±SE)	Median (range)	Proportion of sites present (%)
≥5 cm hollow density	91 (±12) ha^{-1}	55 (0–503) ha^{-1}	85
≥10 hollow density	37 (±7) ha^{-1}	3 (0–286) ha^{-1}	50
Large eucalypt density	66 (±7) ha^{-1}	54 (0–336) ha^{-1}	93

The mean density, standard error, median and range of each variable. The percentage of total sites surveyed where hollows (≥5 cm and ≥10 cm) and large eucalypts were recorded present.

hollows in mesic savannas on Melville Island. The hollow-dependent mammals we studied have been shown to use 2–6 dens in a fortnightly period, overlap in home range, and often use hollows of similar attributes (Penton et al., 2020b, 2021). Northern Australian arboreal mammals may also be more socially tolerant (Kerle, 1998), allowing them to adapt their denning behavior (e.g., increase their propensity to share dens) in areas where hollows are limiting (Banks et al., 2011). All three species use dens other than tree hollows, including hollow logs on the ground, the canopy of the arborescent monocotyledon *Pandanus spiralis*, and dreys (nests of dried leaves and twigs; Griffiths et al., 2001; Firth et al., 2006b; Penton et al., 2020b). Anecdotal evidence suggests that arboreal mammals were in higher abundance prior to European arrival across northern Australian savannas (Woinarski et al., 2011). In areas containing lower densities of hollow-bearing trees, it is likely that alternative den sites may have been used more frequently or at higher rates than recorded more recently. Current threats may be amplified where alternative den uptake is higher (i.e., in areas where hollow densities are lower) as there may be a higher risk of predation or exposure to disturbances such as high intensity fires when denning at or near ground level (Leahy et al., 2016). Therefore, hollow densities below a certain threshold may limit and impact the persistence of populations of hollow-dependent mammals.

The three hollow-dependent mammal species we studied demonstrate varying levels of arboreal behavior, spending time foraging and traveling across the savanna floor due to the open canopy structure of tropical savannas (Friend, 1987; Kerle, 1998; Griffiths et al., 2001; Firth et al., 2006b). The brush-tailed rabbit-rat dens close to the ground or in hollow logs on the ground and spends much of its time foraging for grass seeds (Firth et al., 2005, 2006b; Penton et al., 2020b). Though the black-footed tree-rat dens higher in the canopy (Penton et al., 2021), its reliance on fruiting shrubs, and its large home range (Friend, 1987; Pittman, 2003; Rankmore, 2006) suggests that this species frequently moves across the savanna floor. In comparison, the northern brushtail possum likely spends less time on the savanna floor as it has a smaller home range and does not exhibit large movements across the savanna (Kerle, 1998; Woinarski, 2004; Rankmore, 2006). Irrespective, all three species spend significant amounts of time on the ground foraging and moving across the

savanna floor. The amount of time these species spend on the ground, and their reliance on understory and midstory resources, supports why we found the strongest correlates of abundance to be related to the quality of understory and predator assemblage, rather than the availability of tree hollows.

Despite having undergone a severe decline elsewhere in northern Australia (Woinarski et al., 2010; Stobo-Wilson et al., 2019), it appears that the northern brushtail possum is stable on Melville Island (Davies et al., 2018) even in disturbed areas (i.e., high cat activity and large herbivore presence). This may indicate that the northern brushtail possum is more resilient to these ground-based threats than the two rodent species examined in our study. The northern brushtail possum may spend a greater amount of time in the sub-canopy, as it preferentially feeds on flowers and fruits from *Acacia difficilis*, *Grevillea pteridifolia*, *Acacia bivenosa*, and *Ficus* spp. (Kerle and Burgman, 1984; Cruz et al., 2012). Historically, the distribution of the northern brushtail possum included areas of relatively low productivity. Although in more recent decades the contraction to higher rainfall areas of northern Australia and patchy distribution of northern brushtail possum populations has been attributed to a reliance on less disturbed areas that support dense and diverse foliage (Kerle and Burgman, 1984; Stobo-Wilson et al., 2019). Thus, while the decline of the northern brushtail possum on the mainland has been less severe than that of the rodents, it seems to be negatively affected by similar threats – most likely cat predation and reduction in habitat complexity – in the long-term.

The two rodent species in our study (black-footed tree-rat and brush-tailed rabbit-rat) may be particularly vulnerable across northern Australia because they are reliant on multiple vegetation strata, namely a shrubby understory and overstorey of hollow-bearing trees (Friend, 1987; Firth et al., 2006b; Penton et al., 2020b), and because they respond negatively to ground-layer disturbances including fire (Davies et al., 2017) and large herbivores. This habitat use will limit these species to areas with little disturbance to access adequate food resources and shelter. Simplification of understory habitat by overgrazing and frequent high-intensity fires likely reduces the availability of food resources while increasing the exposure of mammals to predation (Leahy et al., 2016; Legge et al., 2019). Native rodents may be more susceptible to feral cat predation as they represent the majority of native mammals killed Australia-wide, with this offtake strongly concentrated in northern Australia (Pearre and Maass, 1998; Murphy et al., 2019). Disturbances such as high-intensity fire and heavy grazing by feral herbivores can offer significant advantages to feral cats by simplifying the understory, increasing hunting efficiency (Davies et al., 2020; Stobo-Wilson et al., 2020a,b). Feral herbivores may also create "game trails," which facilitate the movement of cats and dingoes through the savanna (Leahy et al., 2016; McGregor et al., 2016; Davies et al., 2020). The question of why semi-arboreal and arboreal mammals have been disproportionally represented among declining mammals in northern Australia has not yet been resolved by this study. It is clear from our results that simply maintaining high densities of hollows in places such as Melville Island may not be sufficient to prevent further decline of hollow-dependent mammals.

Implications for Future Research and Management

Due to the higher densities of hollow-bearing trees on Melville Island compared to the mainland (Woolley et al., 2018), we are unable to speculate as to whether the depletion of tree hollows has contributed to the broad-scale decline of arboreal mammals in northern Australia. Frequent late dry-season fires have been shown to impact the density of suitable hollows for the threatened Gouldian finch (*Erythrura gouldiae*) in northern Australia (Radford et al., 2021). In habitats with low hollow densities, the frequent utilization of alternative dens (e.g., hollow logs, *Pandanus spiralis*) may expose individuals to greater predation risk and impact breeding success, particularly after fire (Leahy et al., 2016; Penton et al., 2020b). Future research should evaluate how mammal abundance varies with hollow availability across larger spatiotemporal scales to address whether frequent high-intensity fires have contributed to the dramatic decline of hollow-dependent arboreal species in northern Australia. Manipulative experiments using nest boxes could also provide insights into whether an increase in denning resources leads to an increase in native mammal abundance.

It is essential that the conservation management of native mammals in tropical savannas focuses on maintaining a complex and diverse understory. Studies on the northern Australian mainland have shown shrub density is strongly influenced by fire regimes, with frequent, high-intensity fires tending to reduce shrub density (Edwards et al., 2003, 2018; Russell-Smith et al., 2003). The impacts of which are also likely exacerbated by high feral herbivore densities (Legge et al., 2019). There needs to be a greater exploration of how frequent fires, even those of low intensity, influence vegetation structure and diversity, especially in relation to the shrub and grass layers, which provide critical shelter from predators and also provide food resources (e.g., fruits, flowers, and seeds; Bowman, 1988; Fensham, 1990; Paramjyothi et al., 2020). In the relatively intact savannas of northern Australia, such as Melville Island, management should aim to conserve hollow-bearing trees while retaining dense and complex under-and mid-story vegetation, which appears to be essential for the conservation of hollow-dependent arboreal mammal species.

DATA AVAILABILITY STATEMENT

The raw data supporting the conclusions of this article will be made available by the authors, without undue reservation.

ETHICS STATEMENT

The animal study was reviewed and approved by permission for animal use was authorized by the Charles Darwin University Animal Ethics Committee (A16002) and the Northern Territory Department of Flora and Fauna (Permit to Interfere with Protected Wildlife No. 58472).

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APPENDIX

Appendix 1 | Comparison of the nightly probability of detection and the overall probability of detection (over 36–53 nights) for the null model (where relative abundance and detectability parameters are assumed to be constant across all survey sites) and the most parsimonious Royle–Nichols occupancy model.

Species	Model	Night detection probability (P) (±SE)	Overall detection probability
Brush-tailed rabbit-rat	Null model	0.10 (±0.02)	0.99
	Best model	0.04 (±0.04)	0.86
Black-footed tree-rat	Null model	0.11 (±0.01)	0.99
	Best model	0.10 (±0.01)	0.99
Northern brushtail possum	Null model	0.13 (±0.01)	0.99
	Best model	0.10 (±0.01)	0.99