Top-down control of species distributions: feral cats driving the regional extinction of a threatened rodent in northern Australia

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Abstract:

Aim:

To investigate if feral cats influence the distribution of Australia's largest remnant population of the threatened brush-tailed rabbit-rat *Conilurus penicillatus*, and examine whether they influenced the extinction probability of *C. penicillatus* over a 15-year period (2000-2015).

Location:

Melville Island, northern Australia.

Methods:

In 2015, small mammal surveys were conducted at 88 sites across Melville Island, 86 of which had previously been surveyed in 2000-2002. We used single-season occupancy models to investigate correlates of the current distribution of *C. penicillatus*, and dynamic occupancy models to investigate correlates of *C. penicillatus* local extinction.

<u>Results:</u>

Our results show that *C. penicillatus*, which once occurred more widely across the island, is now restricted to parts of the island where feral cats are rarely detected and shrub density is high. Our results suggest that feral cats are driving *C. penicillatus* towards extinction on Melville Island, and hence have likely been a significant driver in the decline of this species in northern Australia more broadly. The impact of feral cats appears to be mitigated by vegetation structure.

<u>Main conclusions:</u>

The ongoing development and implementation of methods to effectively reduce feral cat densities, coupled with the management of landscape processes to maintain shrub density, through fire management and the removal of large exotic herbivores, will contribute substantially to conserving this threatened species. This study demonstrates that the distribution of species can be strongly influenced by top-down factors such as predation, thereby highlighting the importance of including biotic interactions when investigating the distribution of predation-susceptible species.

<u>Keywords:</u>

Australia, *Conilurus penicillatus*, distribution, extinction, feral cats, predation

<u>Introduction:</u>

Knowledge of the current and predicted future distributions of species is paramount for biodiversity conservation (Austin, 2007). While species distribution modelling (SDM) can address various problems in applied ecology and conservation biology, the assumption that distributions are limited primarily by 'bottom-up' factors, such as resource availability, often leads to the omission of potentially important causal factors, such as biotic interactions (Guisan and Thuiller, 2005). For example, introduced predators can exert a strong regulatory force on the distribution of their prey, and the omission of such drivers could severely limit the utility of SDM for species whose distributions

are strongly influenced by 'top-down' factors such as predation by introduced carnivores (Guisan and Thuiller, 2005).

Globally, less than 2% of recent extinctions have been directly attributed to introduced species (Gurevitch and Padilla, 2004). However, in areas with diverse populations of evolutionarily naïve prey, such as those that often occur on islands, the impacts of introduced carnivores on native animal species have been severe (Nogales et al., 2004, Medina et al., 2011). For example, feral cats (*Felis catus*) have contributed to at least 14% of global mammal, bird and reptile extinctions on islands (Medina et al., 2011, Doherty et al., 2015). Island rodents are particularly susceptible to introduced predators (Nogales et al., 2004), being driven to or near extinction on many islands throughout the Caribbean (Clough, 1976), the Galapagos (Patton and Hafner, 1983, Dowler et al., 2000) and north-western Mexico (Tershy et al., 2002).

Australia's long history of geological isolation makes many species particularly susceptible to predation by introduced mammalian predators (Short et al., 2002). Since European arrival, Australia has experienced the highest rate of modern mammal extinction on Earth, with the introduced feral cat and red fox (*Vulpes vulpes*) being implicated as key factors in the majority of these (IUCN, 1996, Short et al., 2002, Woinarski et al., 2014). Since its introduction to Australia, the feral cat has been implicated in the extinction of 19 species, as well as the recent catastrophic declines recorded across northern Australia's savanna landscapes (Johnson, 2006, Woinarski et al., 2011, Fisher et al., 2013, Ziembicki et al., 2014, Woinarski et al., 2014).

Over the past two decades, robust evidence demonstrating the significant impact of feral cats on Australian native mammals has emerged. Feral cats preferentially select small mammals as prey (Kutt, 2012), and native mammal reintroduction programmes have failed due to feral cat predation (Hardman et al., 2016, Short, 2016). Frank et al. (2014) demonstrated that even low densities of feral cats have the ability to rapidly extirpate populations of re-introduced rodents in northern Australia. The impact of feral cat predation on small mammal populations in northern Australia appears to be related to processes that simplify vegetation structure, such as high-frequencies of high-intensity fires and heavy grazing by feral herbivores (Legge et al., 2011a, Lawes et al., 2015a, Leahy et al., 2016).

Recent studies have demonstrated that cats in northern Australia hunt more successfully in structurally simple compared with complex habitats (Oakwood, 2000, McGregor et al., 2015). Despite the evidence that predation by feral cats can strongly influence small mammal populations, no study has directly linked cats with the regional extinctions that have occurred for many small mammal species across northern Australia.

Using two datasets collected 15 years apart, we applied occupancy modelling to investigate if feral cats influence the distribution and decline of the nationally threatened brush-tailed rabbit-rat (*Conilurus penicillatus*), and to investigate the role of habitat structure in its persistence. Our study was conducted on Melville Island (5786 km^2), which represents an excellent model system to study the drivers of small mammal distribution in northern Australia's savanna landscapes. It is one of the last areas in Australia that retains its complete pre-European assemblage of small mammals (Burbidge et al., 2009), despite the prevalence of the hypothesised drivers of small mammal decline elsewhere in northern Australia, including feral cats and large herbivores (water buffalo *Bubalus bubalis* and horses *Equus caballus*), and very high fire frequencies. Melville Island has one of the largest extant population of *C. penicillatus* (Woinarski et al., 2014), which occurred across vast areas of northern Australia at the time of European settlement (Cramb and Hocknull, 2010), but is now almost extinct on the mainland (Firth et al., 2006a, Woinarski et al., 2014). While anecdotal evidence suggests that direct predation by feral cats is a major driver in the decline of *C. penicillatus*, other possible mechanisms related to feral cats, such as disease, may also be contributing to the decline of this species (Woinarski et al., 2014).

We modelled both the current spatial patterns of site occupancy, and change in site occupancy by *C. penicillatus* over a 15 year period (2000-2015) on Melville Island, to test the hypotheses that feral cats are a primary driver of *C. penicillatus* distribution, and that their impact is mitigated by vegetation structural complexity. We predicted that the probability of feral cat detection would be negatively correlated with the current distribution of *C. penicillatus* on Melville Island, and positively correlated with the probability of local extinction of *C. penicillatus* at historic sites. We also predicted that the

current distribution and persistence of *C. penicillatus* on Melville Island would be associated with extensive shrub cover.

Methods:

Study site:

Melville Island, the larger of the two main Tiwi Islands, is located 80 km north of Darwin, in Australia's Northern Territory (Figure 1). The island is of low relief ($\leq$ 103 m above sea level) and experiences a tropical monsoonal climate with a wet season (November–April) in which over 90% of the annual rainfall occurs (Australian Bureau of Meteorology, 2015). There is a substantial rainfall gradient, from 1400 mm in the east, to 2000 mm in the north-west. The major vegetation types are savanna woodlands and open forests dominated by *Eucalyptus miniata, E. tetrodonta* and *Corymbia nesophila*, with a predominantly grassy understorey. Shrub density is highly variable, and studies on the mainland have shown that this is influenced by fire regime (Russell-Smith et al., 2003, Woinarski et al., 2004).

Recent fire mapping of the Tiwi Islands from 2000-2013, estimated that on average, 54% of the open savanna woodland burns annually, with the majority burning in late dry season (i.e. after July 31st) (Richards et al., 2015).

The study species:

C. penicillatus is a predominantly granivorous rodent that dens in tree hollows and hollow logs (Firth et al., 2005, Firth et al., 2006b). It forages mostly on the ground, exposing it to feral cat predation. Its adult body weight (150 g) falls within the so-called 'critical weight range', within which Australian mammals have experienced high-rates of decline (Cardillo and Bromham, 2001, Johnson and Isaac, 2009).

Data collection:

In 2015, small mammal surveys were conducted at 88 sites in savanna forest across Melville Island (Figure 1), 86 of which had previously been surveyed in 2000-2002 (see Firth et al. 2006a). The 2000-2002 surveys followed the now standardised protocol for live-trapping in northern Australia, which involved a 50 x 50 m quadrat with 20 Elliot traps (33 x 10 x 9 cm) spaced equidistantly around the perimeter and four cage traps (56 x 20 x 20 cm) located on each corner. Traps were baited with a mixture of peanut butter, oats and honey, and set for three consecutive nights.

The 2015 surveys used both live-trapping and camera-trapping (at 82 of the sites), and only camera-trapping at the other six sites. Live-trapping followed the 2000-2002 protocol but was conducted over four consecutive nights instead of three, and used eight cage traps and 16 Elliot traps. Camera trapping involved five horizontally facing motion-sensor cameras that were deployed at each site for at least 35 consecutive days. To increase the likelihood of being triggered, each camera was carefully positioned to ensure the base of its bait station was in the centre of the field of view (Gillespie et al., 2015). Bait stations contained a mixture of peanut butter, oats and honey. Vegetation within each camera's field of view was cleared using a fire rake to reduce the chance of false triggers and to reduce the risk posed by fire. Of the five cameras deployed at each site, two were Reconyx™ HC550 Hyperfire white flash cameras (Reconyx Inc., Holmen, USA), while the remaining three cameras were Reconyx™ PC800 Hyperfire Professional infra-red flash cameras (Reconyx Inc., Holmen, USA). All cameras could be triggered 24-hours a day and were set to take three image bursts per trigger, with a one second time delay interval between images. The sensitivity of each camera was set to high, with cameras re-arming instantly after being triggered.

Data analysis:

To model spatial patterns of site occupancy by *C. penicillatus*, we selected predictor variables relating to dingos, fire, rainfall, and habitat, in addition to the probability of feral cat detection, based on results from the literature and recent research on the Tiwi Islands (Geyle, 2015). Dingos were included because of their potential role in suppressing cat activity (Johnson, 2006, Kennedy et al.,

2012), as well as their potential as predators of *C. penicillatus*. Variables relating to sampling methods were also incorporated, including Julian day because of potential seasonal variation in *C. penicillatus* detectability (Geyle, 2015). A full description and justification of the variables included in our analyses can be found in Table 1.

The probability of feral cat detection:

There was clear spatial patterning of feral cat detections across Melville Island (Figure 1). While the spatial clustering of detections could reflect higher densities of feral cats, it is also possible that feral cats were simply more detectable at those sites due to site-specific variability in habitat, cat behaviour and/or sampling efficiency. Unfortunately we could not model the effect of habitat variables on site occupancy by feral cats due to low detectability. Instead we used a range of variables hypothesised to influence the detectability of feral cats to investigate if there was any evidence that spatial patterning of feral cat detections was likely due to higher detectability at those sites. To do this we used occupancy models assuming a constant probability of site occupancy by feral cats across Melville (see Appendix S1 in Supporting Information). We found no evidence that the detectability of feral cats was influenced by any site-specific habitat or sampling characteristics (such as the time of year). The only variable to have a significant influence on feral cat detectability was the distance to the closest cat detection. It is important to note that this analysis does not completely rule out the potential influence of site-specific habitat and/or sampling characteristics on the detectability of feral cats as our data may simply have been too sparse to detect an effect.

Whatever the mechanism driving the spatial patterning of feral cat detections, the significant effect of spatial autocorrelation on the detectability of feral cats needed to be accounted for. As such, to generate the best predictions of the probability of feral cat detection at each site, we used spatially explicit generalised linear models (Murphy et al., 2010), with binomial errors, which use an autocovariate to account for the significant effect of spatial autocorrelation on feral cat detectability.

The models were implemented using the "fields", "ncf" and "raster" packages in the program R (R Development Core Team, 2013). We used the Akaike Information Criterion (AIC) to rank and identify parsimonious models (Burnham and Anderson, 2002). Accounting for spatial autocorrelation improved the explanatory power of the most parsimonious model by 12%, which explained 16% of the variation in cat detections. The model performed well at predicting a higher probability of feral cat detection in and around the areas where cats were actually detected (Figure 1). The area under the receiver operating curve (AUC), calculated using the "pROC" package in R, was 0.77. Models with AUC scores greater than 0.75 are considered useful (Phillips and Dudík, 2008).

Correlates of *C. penicillatus* current distribution:

Single-season occupancy models, which explicitly account for imperfect detection, were used to investigate how each predictor variable (Table 1) correlated with site occupancy by *C. penicillatus*. Single-season occupancy modelling was conducted using only the 2015 camera trapping data in the "unmarked" package in R. Prior to analysis, predictor variables were centred and standardised by subtracting the mean and dividing by the standard deviation (Gelman and Hill, 2006).

Due to the many variables and therefore the large number of possible models, occupancy modelling was applied in a two-step process. First we determined which variables best explained the detectability of *C. penicillatus* by running all combinations of the nine variables we hypothesised might influence detectability (i.e. 512 models). This was done with occupancy constrained to a saturated model of the seven variables we hypothesised might influence site occupancy by *C. penicillatus*. Model selection based on AIC was then used to select the most parsimonious detectability model in the candidate set. The second step involved running all possible combinations of the seven occupancy variables (128 models) with detectability constrained to the most parsimonious model identified in step one. Model selection based on AIC was then used again to determine the best model in the candidate set. Where no single model arose as superior at explaining

the distribution of *C. penicillatus* (i.e. ΔAIC <4), model averaging provided parameter estimates based on the results of multiple models (Burnham and Anderson, 2002).

Once the most parsimonious model with only the main effects was identified, we investigated the possible effect of an interaction between the probability of feral cat detection and both fire activity and shrub density. This was done because processes that simplify the structure of vegetation (such as frequent fire) might amplify the impact of feral cats.

Accounting for imperfect detection provides more realistic, but more imprecise estimates of occupancy (Guillera-Arroita et al., 2014). To gauge how accounting for detectability influenced our occupancy estimates and hence the confidence in our conclusions drawn from these models, we also ran all combinations of the occupancy variables, assuming constant detectability.

We assessed model fit with a goodness-of-fit test based on parametric bootstrapping and Pearson's chi-square statistic. This method repeatedly simulates datasets based on a fitted model, and then evaluates the probability that the observed history of outcomes has a reasonable chance of happening if the model assessed is assumed to be correct (MacKenzie and Bailey, 2004).

Correlates of *C. penicillatus* site extinction:

We used dynamic occupancy modelling to investigate correlates of the dynamic processes associated with changes in site occupancy by *C. penicillatus* from 2000 and 2015 (MacKenzie et al., 2003). Dynamic occupancy modelling was conducted using the original live-trapping data and the 2015 camera trapping data in the "unmarked" package in R. Explanatory variables were centred and standardised prior to analysis.

Recent work based on the original live-trapping data demonstrated that the detectability of *C. penicillatus* on the Tiwi Islands is strongly influenced by the time of year that mammal surveys were conducted and fire frequency, while *C. penicillatus* occupancy is mostly determined by vegetation structural elements that are strongly associated with high rainfall as well as fire frequency (Geyle,

2015). Based on these results we parameterised the sub-model of initial occupancy as: $\psi \sim$ Rainfall + Fire activity. We accounted for variation in detectability due to different survey methods being used in the two years by including year in the sub-model of detectability which was defined as: $p \sim$ Julian day + Year + Fire activity. Initial modelling revealed colonisation probabilities were effectively zero (i.e. sites with a low probability of occupancy in 2000 remained unoccupied in 2015), so the sub-model for colonisation was fixed at zero. The sub-model for site extinction was then parameterised to test the following hypotheses about the correlates of *C. penicillatus* site extinction:

Hypothesis 1: Null (extinction constant across environmental space)

Hypothesis 2: Vegetation structure (Shrub density)

Hypothesis 3: Fire activity

Hypothesis 4: Large herbivores

Hypothesis 5: Feral cats

Hypothesis 6: Feral cats and fire activity

Hypothesis 7: Feral cats and large herbivores

Hypothesis 8: Feral cats and vegetation structure

Hypothesis 9: Feral cats interacting with fire activity

Hypothesis 10: Feral cats interacting with large herbivores

Hypothesis 11: Feral cats interacting with vegetation structure

Model selection based on AIC was used to select the most parsimonious model in the candidate set.

Results:

Correlates of *C. penicillatus* distribution:

While no single model arose as superior (i.e. had a ΔAIC <4), model averaging demonstrated that the probability of feral cat detection was the strongest predictor variable for the distribution of *C. penicillatus* (Figure 2), with *C. penicillatus* detected only at sites at which the probability of detecting a feral cat was $<30\%$ (Figure 3). Where the probability of feral cat detection was $<10\%$, the

probability of site occupancy by *C. penicillatus* tended to be >70% (Figure 3). Shrub density was the only other significant predictor variable (Figure 2), and was positively associated with site occupancy by *C. penicillatus* (Figure 3).

Nightly detectability for *C. penicillatus* was 6.1% at each 5-camera survey site, but due to the length of time the cameras were deployed (minimum of 35 nights), a very high (>93%) probability of overall detection was achieved. Given the overall high detectability, the estimated rate of occupancy by the best model was only slightly greater than the naïve occupancy rate (i.e. the proportion of sites where *C. penicillatus* was detected) and null model occupancy estimate (see Table S1 in Supporting Information) and the predicted impacts of covariates on occupancy were the same regardless of whether or not the models included effects of covariates (including "Julian day") on detectability. There was no evidence that including an interaction between fire and shrubs with the probability of feral cat detection improved the model fit.

Correlates of *C. penicillatus* site extinction:

The probability of feral cat detection, shrub density and large herbivores were clear correlates of *C. penicillatus* site extinction. The four best models (i.e. ΔAIC <4), which incorporated either the probability of feral cat detection and shrub density or the probability of feral cat detection and large herbivore presence, had overwhelming support (Table 2), far superior to the model parameterised with the single main effect of the probability of feral cat detection. The most parsimonious model demonstrated that *C. penicillatus* had virtually no chance of persistence where the probability of detecting a feral cat was >40% (Figure 4). The probability of *C. penicillatus* site extinction was strongly influenced by the density of shrubs; with high shrub density significantly reducing the probability of *C. penicillatus* site extinction (Figure 4).

Discussion:

In an attempt to better understand the decline of small mammals across northern Australia, we modelled the current spatial patterns of site occupancy, as well as the change in site occupancy by *C. penicillatus* over a 15 year period (2000-2015) on Melville Island in northern Australia. Our results demonstrate that *C. penicillatus* was once more widespread on Melville Island but is now restricted to areas with a low probability of feral cat detection and high shrub density, where predation by feral cats is expected to be significantly diminished (McGregor et al., 2015). This study provides the first corroboration from the mesic savannas of the Northern Territory of the hypothesis that a sparse understorey (i.e. lack of shrubs) influences predation by feral cats to drive the decline of small mammals in northern Australia (McGregor et al., 2014, Lawes et al., 2015a, Leahy et al., 2016).

Despite being widespread at the start of the 20th century, the distribution of *C. penicillatus* has now contracted dramatically across mainland northern Australia (Dahl, 1897, Firth et al., 2010, Woinarski et al., 2014). However, *C. penicillatus* has persisted on Melville Island in relatively high numbers, with the island supporting one of the largest remaining populations of this species (Firth et al., 2006a). Due to a lack of historical records (Abbott and Burbidge, 1995), the timing of the introduction of feral cats on Melville Island remains equivocal. It is possible that feral cats arrived with the first British settlement on Melville Island, the short-lived Fort Dundas (1824-28) (Brocklehurst, 1998), however, they may have arrived appreciably later on Melville Island than in other parts of northern Australia. If feral cats were established on Melville Island by the mid-19th century, this poses the question: If feral cats have been a significant driver of *C. penicillatus* decline across northern Australia, why has this species persisted on Melville Island but declined substantially on the mainland? The persistence of *C. penicillatus* on Melville Island can be explained if the predation pressure exerted by feral cats on populations of *C. penicillatus* is mitigated by other environmental factors that vary between Melville Island and mainland northern Australia.

Species distribution modelling by Firth *et al.* (2006a) led to the suggestion that the persistence and "unusually high abundance" of *C. penicillatus* on the Tiwi Islands may be related to more benign fire regimes. Frequent and/or intense fires reduce the survival of *C. penicillatus* and pose a significant threat to the long-term persistence of this species (Firth et al., 2010). Recent fire mapping of the Tiwi

Islands has estimated that an average of 54% of the open savanna woodland is burnt each year, with 65% of the burning occurring in the late dry season (Richards et al., 2015). Russell-Smith et al. (1997) quantified the fire history of Kakadu National Park, where *C. penicillatus* became extinct in the 2000s. They reported that from 1980-94, an average of 55% of Kakadu's lowland savannas was burnt each year, with the majority of burning occurring in the early dry season period. This is similar to the estimates by Russell-Smith et al. (2009) derived for Kakadu for the period 1995-2004, who estimated that on average 50% of the lowland savannas were burnt each year, with 28% of burning occurring in the late dry season. Therefore, at a macro-scale, there is no evidence that the dominant fire regimes on Melville Island have been any less severe than those in areas where *C. penicillatus* has experienced massive declines on the mainland. However, as Melville Island receives a greater amount of dry-season rain, fires regimes at a finer scale may have been significantly less severe than in areas on mainland Australia. Determining how fire regimes differ between Melville Island and mainland Australia warrants further investigation. Studies have demonstrated that small mammal declines occur in the months following a fire, due to a heightened rate of predation as a result of reduced vegetation cover (Leahy et al., 2016). As such, the current persistence of *C. penicillatus* populations on Melville Island is possibly related to more structurally complex vegetation.

Measurements of shrub density in 18 experimental fire plots across Melville Island in 2015, estimated an average of 8,306 stems per hectare for small shrubs (<50 cm), and 5,939 stems per hectare for medium shrubs (50 cm to 2 m) (Anna Richards, unpublished data). These figures dramatically exceed shrub densities reported from analogous parts of the adjacent mainland (Kakadu, Litchfield and Nitmiluk National Parks) of 3,258 stems per hectare for small shrubs (<50 cm) and 802 stems per hectare for medium shrubs (50 cm to 2 m) (Russell-Smith et al., 2010). The exceptionally high shrub density recorded on Melville Island likely reflects the high productivity of the ecosystem (Richards et al., 2012). Not only does Melville Island sustain a more structurally complex understorey, evidence suggests that the rate of vegetation recovery after a fire event may also be greater than in less productive areas (Michelle Freeman, unpublished data). The length of time *C. penicillatus* is exposed to the heightened risk of predation following a fire event is likely to be shorter on Melville Island than

in less productive areas. Our results demonstrate that shrub density is negatively, and the presence of large herbivores positively, associated with the probability of *C. penicillatus* site extinction. These results support the hypothesis that feral cats hunt less efficiently in areas with a dense understorey. There is evidence that large herbivores in northern Australia may simplify vegetation structure in a way that exposes small mammals to a greater risk of predation (Legge et al., 2011a). In our study, large herbivores were more likely to be present in areas with low shrub density. The role that large herbivores play in influencing vegetation structure in northern Australia, and the possible flow-on effects on small mammal populations, should be the focus of future research.

While the current persistence of *C. penicillatus* on Melville Island is likely due in part to high productivity mitigating the top-down impacts of feral cat predation through vegetation structure, the bottom-up influences of high productivity have also likely contributed to the persistence of *C. penicillatus* on Melville Island. Shrub density was positively associated with site occupancy by *C. penicillatus* irrespective of the probability of feral cat detection, possibly indicating the importance of productivity driven resource availability. The high availability of critical resources on Melville Island such as tree hollows, hollow logs and perennial grasses (Crowley, 2008, Woinarski and Westaway, 2008), may result in increased breeding rates and high abundance, thereby offering *C. penicillatus* populations greater overall resilience to feral cat predation. The resilience of small mammal populations to feral cat predation may also vary spatially across Melville Island itself. This not only explains the pattern of site persistence and extinction of *C. penicillatus*, but possibly explains the spatial pattern of feral cat detections. If feral cat predation has effectively reduced prey availability in areas with low population resilience, cats in these areas may now be required to increase their foraging activity thus making them more detectable.

Evidence suggests that *C. penicillatus* was one of the first species to exhibit decline on mainland northern Australia, followed by declines of a wide range of small mammal species (Woinarski et al., 2010). It is possible that the change in *C. penicillatus* populations reported here for Melville Island reflects the pattern of earlier decline on mainland northern Australia. If this is the case, Melville Island may soon be facing the same pattern of severe declines of a range of small mammal species.

Whether or not history repeats itself will likely depend on the management response and investment in ongoing monitoring and research.

Currently there are few feasible methods for the direct management of feral cats at large spatial scales (Nogales et al., 2004, Hardman et al., 2016). The applicability and effectiveness of each method is greatly influenced by a range of factors depending on the environment in which cat control is being undertaken (see Hardman et al., 2016 and references therein). Globally, feral cats have been eradicated from at least 100 islands, with most successful eradications using a combination of control methods (Nogales et al., 2004, DIISE, 2015). The majority of islands from where feral cats have been eradicated have been small (<5 km^2), to date the largest island from which feral cats have been successfully eradicated is subantarctic Marion Island (290 km^2) (Bester et al., 2002, Nogales et al., 2004). Melville Island is an order of magnitude larger (5788 km^2), making complete feral cat eradication a formidable task. While the ongoing development of effective feral cat control measures may make feral cat eradication from Melville Island a more realistic objective in the future, reducing the adverse impacts of feral cats in areas of high conservation value (i.e. around remnant populations of *C. penicillatus*) could be a feasible and effective immediate management option. The benefits to small mammal populations from any direct management of feral cats may be amplified when implemented concurrently with landscape management that enhances vegetation structure (McGregor et al., 2014).

CSIRO's Tiwi Carbon Study (Richards et al., 2012), recorded an increase in shrub density in response to reduced fire frequency on Melville Island (Anna Richards, unpublished data). Fire management that reduces the frequency of fire could therefore be a viable management option to reduce the impact of feral cats by enhancing shrub-layer complexity on Melville Island. The EcoFire project established a strategic regional prescribed burning programme in the Kimberley region of Western Australia, which aimed to increase the heterogeneity of vegetation age and structure, and the amount of old-growth vegetation (3 years or older) (Legge et al., 2011b). Biodiversity indicators (including small mammal species richness and abundance) collectively showed an improvement in response to the applied fire management. Similar to fire, large introduced herbivores also have the potential to reduce

the complexity of understorey vegetation in the mesic savannas of northern Australia, and studies have demonstrated the recovery of small mammal populations following de-stocking (Legge et al., 2011a). The ongoing development of effective direct cat control methods, coupled with the management of landscape processes to maintain shrub density, through fire management and the removal of large exotic herbivores, are likely to contribute substantially to conserving *C. penicillatus* on the Tiwi Islands. Whether such management can be useful across northern Australia's vast savanna landscapes is much less certain, given the complexity of interactions between fire, exotic herbivores and vegetation cover – and that these processes are highly context-specific. There is unlikely to be a 'one-size-fits-all' approach to managing landscape processes (e.g. fire, grazing) for small mammal conservation.

Conclusion:

Predation pressure by feral cats, and its association with vegetation structure, was the most plausible reason for explaining the persistence and decline of a mammal species of significant conservation concern. Our study has highlighted that the ongoing monitoring of threatened species is crucial for their conservation. Ongoing monitoring greatly increases our understanding of the causal factors of decline, allowing the development of effective management strategies for species conservation. The identification of such causal factors also has important implications for the use of species distribution modelling in the context of biodiversity conservation, when such models assume a primacy of bottom-up factors. Our findings reinforce the need to include all important factors based on current ecological theory when predicting species distributions (Austin, 2002, Guisan and Thuiller, 2005).

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Biosketch:

The researchers involved in this publication have a wide-range of expertise, including mammalogy, fire-ecology and applied statistics. Our research group highlights how collaborative, trans-disciplinary research can produce significant advancements towards the conservation of biodiversity.

Author contributions:

H. D., B. M., M. M., A. A., G. G. and E. N. conceived the ideas; H. D., B. M., J. W., R. F. and H. G. collected the data; H. D. and B. M. analysed the data, and H. D., B. M., M. M., A. A. and G. G. led the writing.

Supporting Information:

Additional supporting information may be found in the online version of this article:

Appendix S1 {Detectability correlates of feral cats on Melville Island}

Table S1 {Occupancy and detectability estimates of *Conilurus penicillatus* on Melville Island}

Tables:

Table 1: Description and justification of the variables used in analyses to assess the drivers of *Conilurus penicillatus* distribution and site extinction on Melville Island.

Explanatory variable	Description and justification for inclusion	Variable used in analyses to predict:
Fire activity	Following Lawes et al. (2015), a remote-sensed fire variable derived from fine-scale (30 x 30 m) LANDSAT satellite imagery, representing the proportion of the area surrounding each site that was burnt in each year, averaged over the five years preceding mammal sampling. Calculations were made using an area with a radius of 3.2 km as shown by Lawes et al. (2015b) to have the strongest influence on small mammal populations.	• Probability of feral cat detection • *C. penicillatus* distribution • *C. penicillatus* extinction
Rainfall	Mean annual rainfall (Australian Bureau of Meteorology, 2015). Throughout Australia, feral cat densities tend to be lower in areas of high rainfall (S. Legge and J. Woinarski, unpublished data) and mammal species in areas of high rainfall have declined the least (Fisher et al., 2013).	• Probability of feral cat detection • *C. penicillatus* distribution
Dingo activity	The proportion of nights that dingos were recorded on camera at each site. This was taken as an approximation of dingo activity at each site. Included in analyses to investigate the potential negative influence of dingos on feral cats and potential benefits for small mammal populations (Johnson, 2006, Kennedy et al., 2012).	• Probability of feral cat detection • *C. penicillatus* distribution
Shrub density	A count of the number of shrubs in a 1 x 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 less than 5 cm. Shrubs with multiple stems were counted as a single individual. Vegetation structure has been demonstrated to reduce feral cat hunting success, and therefore could influence the distribution of feral cats as well as the occupancy and detectability of small mammals (McGregor et al., 2015).	• Probability of feral cat detection • *C. penicillatus* distribution • *C. penicillatus* extinction
Distance to water	A remote-sensed variable measuring the distance (m) from each site to the closest permanent water body. The distance to water was demonstrated by Firth et al. (2006a) to strongly influence a number of small mammals on Melville Island.	• *C. penicillatus* distribution
Coarse woody debris (CWD)	A count of the number of logs with a diameter of greater than 5 cm that crossed a 200 m long transect at each site. Included in analyses due to Firth et al. (2006b) demonstrating the reliance of *C. penicillatus* on fallen logs as den sites.	• *C. penicillatus* distribution
Probability of feral cat detection	As an index of feral cat activity, we used the predicted probability of detecting feral cats at each site, derived from spatially explicit generalised linear models (Murphy et al., 2010). The probability of feral cat detection was included in the analyses as cats have been implicated as a major factor in the northern mammal decline (Woinarski et al., 2011, Ziembicki et al., 2014).	• *C. penicillatus* distribution • *C. penicillatus* extinction
Feral herbivore presence	A binary variable indicating the presence or absence of large feral herbivores at each site. Feral herbivores were the introduced water buffalo (*Bubalus bubalis*) and horse (*Equus caballus*). Feral herbivores potentially influence small mammal populations via impacts on vegetation structure (Legge et al., 2011a).	• *C. penicillatus* extinction
Julian day	The Julian day of the calendar year that sampling started at each site. Recent work by Geyle (2015) demonstrated that the detectability of *C. penicillatus* increases throughout the dry season.	• *C. penicillatus* distribution • *C. penicillatus* extinction
Number of cameras operating	An observation level covariate to account for the variation in detectability arising from uneven numbers of cameras operating at different sites due to camera malfunction and destruction.	• *C. penicillatus* distribution
Year	Year was included in the dynamic occupancy models to account for the variation in detectability arising from the different survey methods used in the two years.	• *C. penicillatus* extinction

Table 2: Model selection results for dynamic occupancy models fit to test competing hypotheses of the drivers of *Conilurus penicillatus* site extinction. *K* indicates the number of parameters; w_i is the Akaike weight; ΔAIC represents the difference between the model's AIC value and that of the top-ranking model. *ψ* denotes occupancy, *γ* denotes colonisation, *ε* denotes extinction and *p* denotes detectability. Bold text indicates the four best models.

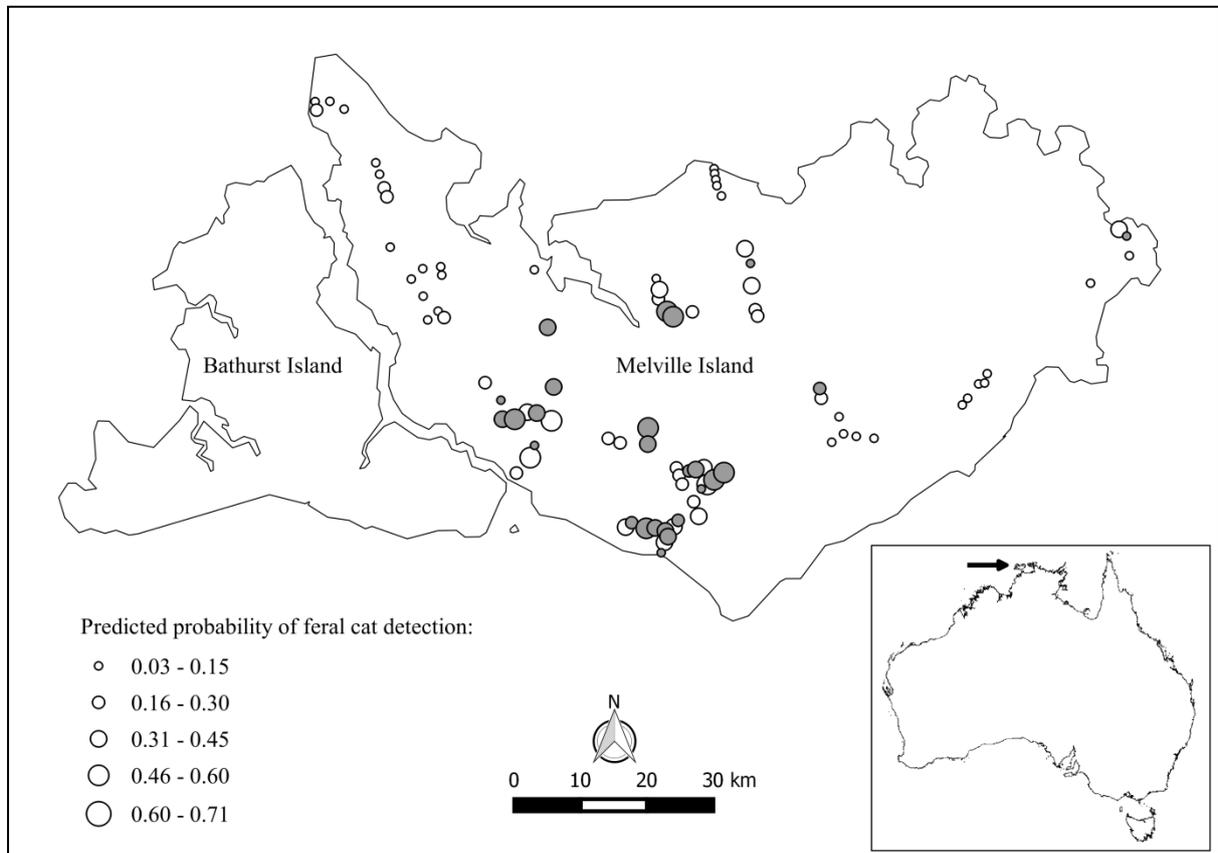| Model	K	ΔAIC	w_i
H1: Null extinction	9	34.45	0.00
ψ (Rainfall + Fire activity) *γ* (~1) *ε* (~1) *p* (Julian day + Year + Fire activity)			
H2: Vegetation structure	10	25.39	0.00
ψ (Rainfall + Fire activity) *γ* (~1) *ε* (Shrub density) *p* (Julian day + Year + Fire activity)			
H3: Fire activity	10	21.21	0.00
ψ (Rainfall + Fire activity) *γ* (~1) *ε* (Fire activity) *p* (Julian day + Year + Fire activity)			
H4: Large herbivores	10	20.59	0.00
ψ (Rainfall + Fire activity) *γ* (~1) *ε* (Large herbivores) *p* (Julian day + Year + Fire activity)			
H5: Feral cats	10	16.46	0.00
ψ (Rainfall + Fire activity) *γ* (~1) *ε* (Feral cat detection) *p* (Julian day + Year + Fire activity)			
H6: Feral cats interacting with fire	12	12.60	0.00
ψ (Rainfall + Fire activity) *γ* (~1) *ε* (Feral cat detection * Fire activity) *p* (Julian day + Year + Fire activity)			
H7: Feral cats and fire	11	12.38	0.00
ψ (Rainfall + Fire activity) *γ* (~1) *ε* (Feral cat detection + Fire activity) *p* (Julian day + Year + Fire activity)			
H8: Feral cats interacting with large herbivores	**12**	**3.58**	**0.09**
ψ (Rainfall + Fire activity) γ (~1) ε (Feral cat detection * Large herbivores) p (Julian day + Year + Fire activity)			
H9: Feral cats and large herbivores	**11**	**2.33**	**0.17**
ψ (Rainfall + Fire activity) γ (~1) ε (Feral cat detection + Large herbivores) p (Julian day + Year + Fire activity)			
H10: Feral cats interacting with vegetation structure	**12**	**1.82**	**0.21**
ψ (Rainfall + Fire activity) γ (~1) ε (Feral cat detection * Shrub density) p (Julian day + Year + Fire activity)			
H11: Feral cats and vegetation structure	**11**	**0.00**	**0.53**
ψ (Rainfall + Fire activity) γ (~1) ε (Feral cat detection + Shrub density) p (Julian day + Year + Fire activity)			

Figures:

Figure 1: Location of the 88 sites surveyed for small mammals in 2015 on Melville Island, the largest of the Tiwi Islands. The location of Melville Island relative to mainland Australia is shown in the inset. The diameter of the circles is proportional to the predicted probability of detecting a feral cat, based on the most highly-ranked spatial generalised linear model, ranging from 0.03 to 0.71. Filled circles indicate sites where feral cats were detected, open circles indicate non-detection.
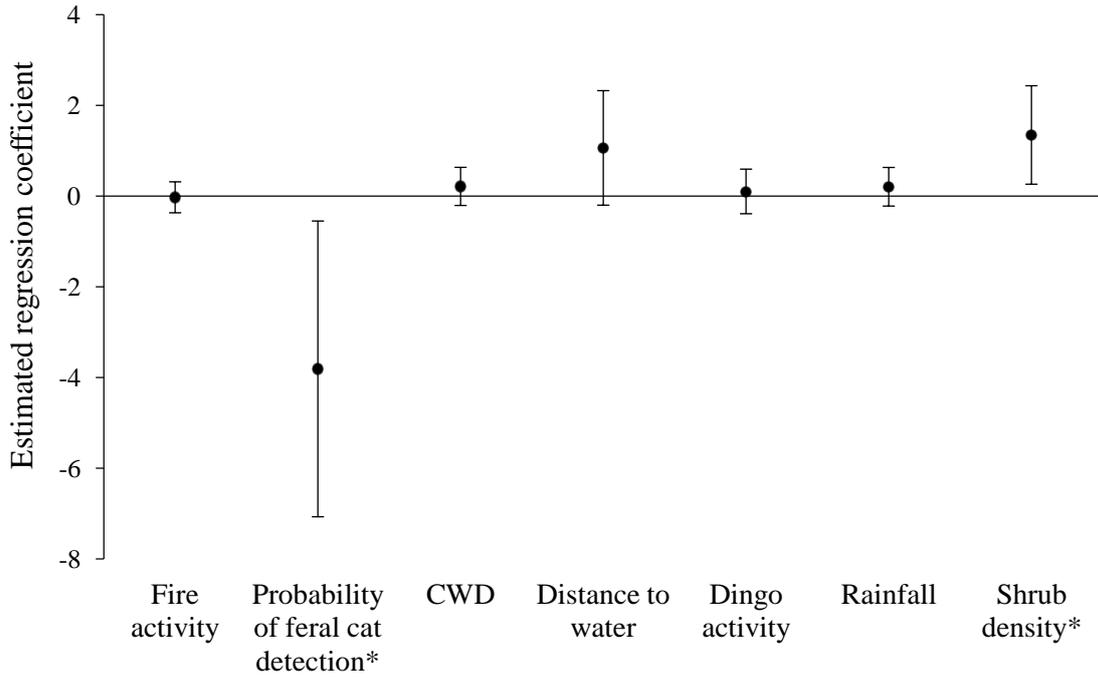
Figure 2: Model averaged regression coefficient estimates for *Conilurus penicillatus* occupancy. Error bars indicate 95% confidence intervals; asterisks indicate where they do not overlap zero.
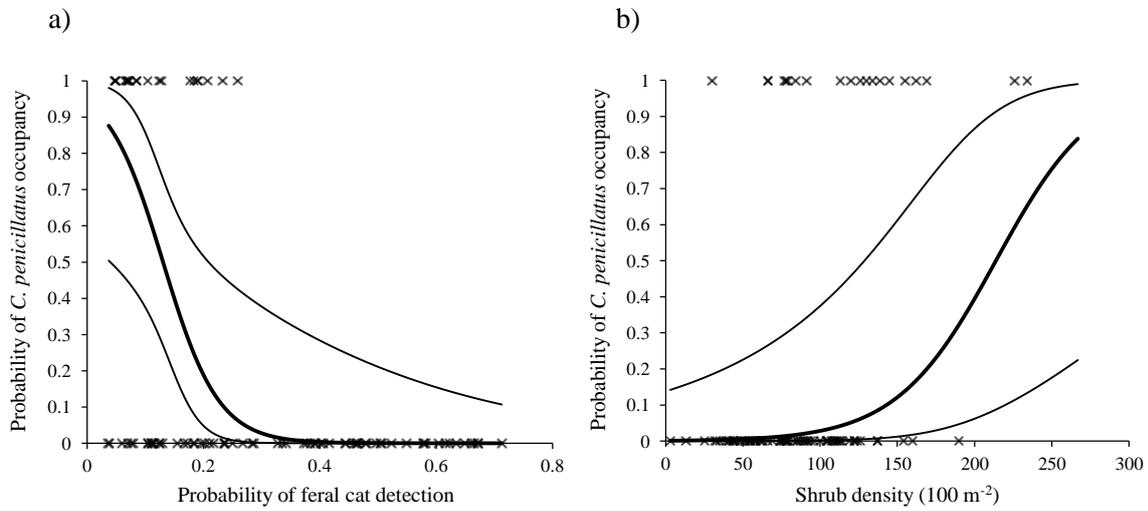

Figure 3: Modelled relationship between a) the probability of feral cat detection b) the density of shrubs and the probability of site occupancy by *Conilurus penicillatus*. Thin lines indicate 95% confidence intervals. Crosses indicate observed data.
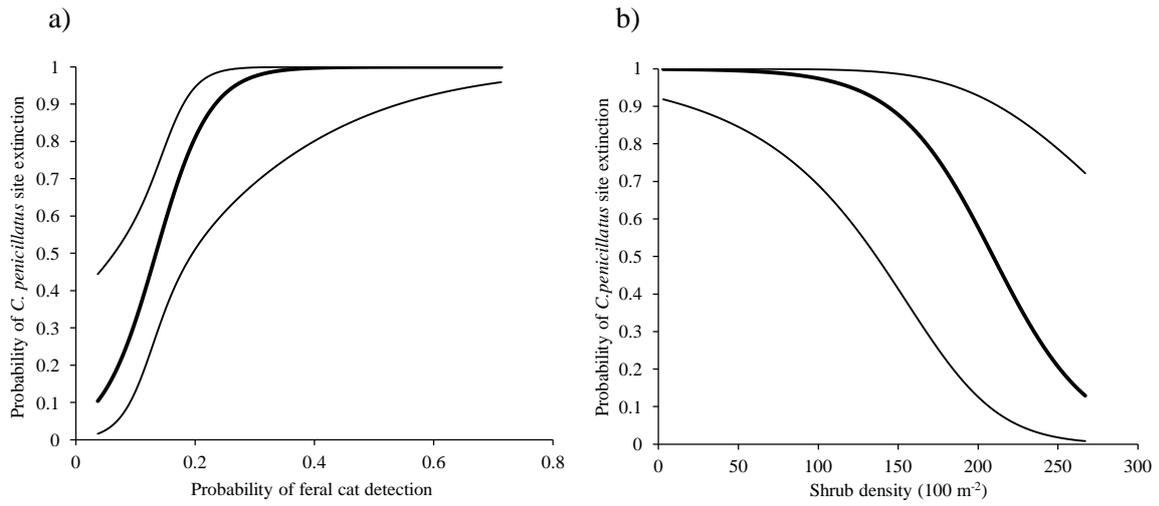
Figure 4: Modelled relationship between a) the probability of feral cat detection b) the density of shrubs and the probability of *Conilurus penicillatus* site extinction. Thin lines indicate 95% confidence intervals.

Appendix S1: Detectability correlates of feral cats on Melville Island

The model:

The following model assumes constant occupancy across Melville Island to investigate whether rainfall, fire, vegetation structure, dingos, time of year, camera malfunctions or the distance to the nearest site with a cat detection had a significant influence on the detectability of feral cats through the data collection in 2015:

Model: occu(~Rainfall + Fire activity + Shrub density + Dingos + Time of year + Number of cameras operating + Distance to nearest cat detection ~ 1)

Results:

Model:

Occupancy:

Estimated	SE	z	P(>|z|)
1.07	1.09	0.976	0.329

Detection:

	Estimate	SE	z	P(>|z|)
Intercept	-5.0717	1.894	-2.6783	0.0074
Rainfall	-0.0623	0.469	-0.1328	0.8943
Fire activity	0.0475	0.232	0.2046	0.8379
Shrub density	0.1561	0.216	0.7215	0.4706
Dingos	-0.3100	0.381	-0.8131	0.4161
Time of year	-0.0365	0.400	-0.0911	0.9274
Number of cameras operating	0.1342	0.389	0.3446	0.7304
Distance to nearest cat detection	-0.9091	0.409	-2.2236	0.0262*

Conclusion:

There is no evidence in our dataset that the detectability of feral cats was significantly influenced by site-specific habitat or sampling characteristics, however there is evidence of significant spatial autocorrelation.

Table S1: Occupancy and detectability estimates of *Conilurus penicillatus* on Melville Island

Table S1: ΔAIC values for the null model (where occupancy and detectability parameters are assumed to be constant across all survey sites), and the most parsimonious models for *Conilurus penicillatus*. Estimates of occupancy, nightly detectability, and the probability of overall detection given the average number of camera trap nights are also shown. The naïve occupancy estimate (i.e. the proportion of sites where *C. penicillatus* was detected) is also shown.

Species	Model	ΔAIC	Occupancy (Ψ) ($\pm$ SE)	Nightly detectability (p) ($\pm$ SE)	Probability of overall detection
Conilurus penicillatus					
	Naïve	-	0.23	-	-
	Null model	88.6	0.23 (0.05)	0.11 (0.01)	0.99
	Best model	0.0	0.27 (0.08)	0.06 (0.03)	0.93