Apex predator suppression is linked to restructuring of ecosystems via multiple ecological pathways

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ABSTRACT

Removal of apex predators can drive ecological regime shifts owing to compensatory positive and negative population level responses by organisms at lower trophic levels. Despite evidence that apex predators can influence ecosystems though multiple ecological pathways, most studies investigating apex predators' effects on ecosystems have considered just one pathway in isolation. Here, we provide evidence that lethal control of an apex predator, the dingo *Canis dingo*, drives shifts in the structure of Australia's tropical-savannah ecosystems. We compared mammal assemblages and understorey structure at seven paired-sites. Each site comprised an area where people poisoned dingoes and an area without dingo control. The effects of dingo control on mammals scaled with body size. Where dingoes were poisoned, we found greater activity of herbivorous macropods and feral cats, a mesopredator, but sparser understorey vegetation and lower abundances of native rodents. Our study suggests that ecological cascades arising from apex predators' suppressive effects on herbivores and mesopredators occur simultaneously. Concordant effects of dingo removal across tropical-savannah, forest and desert biomes suggest that dingoes once exerted ubiquitous top–down effects across Australia and provides support for calls that top–down forcing should be considered a fundamental process governing ecosystem structure.

Keywords: *Canis dingo*, mesopredator release hypothesis, trophic cascade, tropical ecosystems

INTRODUCTION

Apex predators can play a pivotal role in structuring ecosystems through both their direct and indirect effects on other species (Estes, et al. 2011). Apex predators can exert “direct” effects on their prey and competitors by instilling fear and directly killing them (Creel and Christianson 2008, Switalski 2003). Consequently, apex predators can limit populations of large herbivores and smaller predators and induce shifts in their behaviour, diet and physiology (Creel and Christianson 2008, Switalski 2003). The strong effects that apex predators exert on the abundance and behaviour of their prey and competitors can result in “trophic cascades” of indirect effects that become manifest as shifts in the demography and phenotypes of species that may have only weak or no direct interactions with apex predators . Such indirect effects can arise due to a myriad of possible pathways and often but not exclusively occur when species that interact strongly with large herbivores or mesopredators are themselves released from predation or competition. However, despite evidence that trophic cascades initiated by apex predators can be an over-riding factor shaping some ecosystems, debate remains regarding whether predators’ top-down effects should be regarded as ubiquitous and fundamental factors shaping ecosystems or as context dependent anomalies .

Theory predicts that apex predators can structure ecosystems through a multitude of ecological pathways (Estes, et al. 2011, Ripple, et al. 2014). Trophic cascade theory predicts that loss of apex predators from ecosystems will lead to the irruption of herbivores and diminished plant biomass by reducing the intensity of herbivory (Schmitz, et al. 2000). The mesopredator release hypothesis (MRH), predicts that reduced abundance of top-order predators will result in increased abundance or activity of smaller predators (mesopredators) and subsequent declines in the abundance of the prey of mesopredators (Crooks and Soule 1999). Top-down effects of apex predators can also indirectly influence the abundances of species at lower trophic levels by altering the balance of competitive relationships between species at lower trophic levels (Paine 1980). Despite evidence that apex predators can influence ecosystems via multiple ecological pathways, most studies investigating apex predator effects on ecosystems have considered just one pathway in isolation (Estes, et al. 2011, Ripple, et al. 2014). However, apex predators likely exert simultaneous effects along multiple ecological pathways. Thus, removal of apex predators can potentially trigger ecological regime shifts owing to compensatory positive and negative population level responses by organisms along myriad interaction pathways (Colman, et al. 2014)Australia's largest terrestrial predator is the dingo (*Canis dingo*, also known as wild dog; 12–22 kg; (Crowther, et al. 2014)). In the savannahs of Australia's northern tropics, dingo eradication programs provided us with the opportunity to conduct a large-scale, 'natural' experiment to examine the role that apex predators have in structuring ecosystems. In this region, dingo populations are controlled because they attack livestock. The most widely used method to kill dingoes in this region is the distribution of meat baits containing the poison 1080 (Fleming, et al. 2001). Studies from arid and forested regions in southern Australia provide evidence that dingoes structure ecosystems through trophic cascades arising from the suppressive effects that they have on populations of herbivorous kangaroos and wallabies (Family, Macropodidae) and introduced mesopredators, the red fox (*Vulpes vulpes*) and feral cat (*Felis catus*) (Colman, et al. 2014, Letnic, et al. 2009, Morris and Letnic 2017). Studies from southern Australia show that dingoes' effects on mammal species scale with body size, whereby mammals with body masses <5500 g tend to decrease in abundance and mammals with body masses >5500 g increase in abundance (Hunter, et al. 2018). Large mammals are thought to decline in abundance due to direct predation from dingoes whilst small mammals are thought to benefit indirectly from dingoes' suppressive effects on mesopredators and herbivores (Hunter et al. 2018). However, understanding of dingoes' effects on ecosystems in tropical Australia is limited (Brook, et al. 2012, Corbett 1995, Kennedy, et al. 2012, Radford, et al. 2014).

Applying trophic cascade theory, the mesopredator hypothesis and knowledge from studies on the effects of dingo removal conducted in southern Australia we predicted that the effect of dingo control should alternate with trophic group and scale with body size. The red fox does not occur in northern Australia so they are not included in this study. Specifically, we predicted: (i) higher abundances of herbivorous macropods (Macropus spp., 15 - 64 kg, and wallabies, 4.5 – 9 kg) and the feral cat (2.5 - 6.5 kg) in areas with dingo control because these species would experience less predation or harassment; (ii) lower abundances of rodents (15 - 700 g), in areas with dingo control owing to enhanced predation and habitat disturbance from mesopredators and macropods, respectively; and (iii) decreased complexity of understorey vegetation structure in areas subjected to dingo control owing to increased consumption by abundant large herbivores. We tested our predictions by comparing mammal species abundances and activity and understorey vegetation density at seven paired locations in the northern tropics of Australia (Supplementary information Fig. S1). Each pair of sub-sites consisted of an area subjected to dingo control and an area with similar environmental attributes and land-use that lacked dingo control. We treated each paired site as an independent comparison and then pooled results using a meta-analytic approach to determine the effects of dingo control on response variables (Colman, et al. 2014). We then used structural equation modelling (SEM) to further investigate the hypothesised direct and indirect relationships among the response variables.

MATERIALS AND METHODS

Study sites

We conducted our research at seven paired sites (Supplementary information Fig. S1) in the *Eucalyptus*-dominated savannahs of the wet-dry tropics of northern Western Australia and Northern Territory (Brock 2001). The natural vegetation of our study sites had not been cleared, but had been subject to varying levels of disturbance by fire, and grazing by domestic and feral livestock. . The predominant land-uses in Northern Australia are traditional indigenous uses, rangelands and conservation reserves. The principal technique used by pastoralists and government authorities to suppress dingo populations in this region is the distribution of poisoned meat baits containing 6 mg of the toxin sodium fluoroacetate (compound 1080) (Kennedy, et al. 2014). Baits are typically distributed at places where cattle come to water or from the air via light aeroplane (Kennedy, et al. 2014). Baiting is also complemented by shooting of dingoes. Baiting using the toxin 1080 was introduced in the 1960s in Western Australia and the late 1970s in the Northern Territory (Fleming, et al. 2001). Since useage of the 1080 toxin commenced in northern Australia, the number of baits distributed each year in each jurisdiction has steadily increased (Supplementary information Fig. S2). Prior to the introduction of the 1080 poison, strychnine was used as a toxin in meat baits laid for dingoes (Fleming, et al. 2001). Dingo baiting programs have little effect on cat populations because cats display strong preferences for bait presentation and rarely consume the types of baits laid for dingoes ((Doherty, et al. 2017)).

The study region has a monsoonal climate characterized by a hot humid wet season (December–March) and a hot dry season (April–November). Nearly all precipitation falls in the wet season. Mean annual rainfall at the study sites ranges between 800 - 1800 mm, with a maximum average monthly temperature of 27 - 32° C (source: Australian Bureau of Meteorology).

Each of the seven study sites consisted of a pair of sub-sites, six of the seven pairs were located less than 100 km apart (Supplementary information Fig. S1), however, due to logistical constraints one pair was 180 km apart. Each pair of sub-sites consisted of a sub-site that was subject to a minimum of 2 consecutive years of dingo control and a sub-site not subjected to consistent dingo control. We determined baiting regimes by consulting with pastoralists and government staff involved in deploying 1080 baits and administering the use of1080 poison.

We selected sub-sites based on similar vegetation types, landforms and annual rainfall (rainfall differences = < 1 mm; Table S1 in Supporting Information). Sub-sites were also matched for land-use so that comparisons were made between pastoral properties where livestock were grazed commercially or between properties not used for commercial livestock production that were used for the purposes of traditional indigenous land-use, safari hunting of feral livestock or conservation reserve. We sampled each paired site once within the same two-week period and season, and assumed similar landscape characteristics and climate of the sub-sites within each pair. We sampled all paired sites during the dry season months (April – November) between 2012 - 2014. We tested similarity of rainfall history between paired subsites by comparing differences in recent and long-term rainfall (Table S1 in the electronic supplementary material). We found no significant differences in rainfall over the previous six months (paired t-test, $t = 1.94$, df = 6, $P = 0.13$), or long-term annual rainfall (paired t-test, $t = 1.94$, df = 6, $P = 0.34$).

Mammal Abundance and vegetation assessments

At each sub-site, we measured the activity of predators (dingoes and feral cats) using 24 track detection stations placed at 1 km intervals along unpaved vehicle tracks (Funston, et al. 2010). At each station we swept the road flat at a width of 5 m. Roads were chosen based on their proximity to the trapping grids and continuity throughout the sub-site. Each morning for three consecutive nights, we checked for tracks at the stations. As cats do not commonly walk along roads we checked an additional 50 m for cat tracks using the previous day's tyre tracks as a marker, tracks occurring outside the tyre marker were not included. We created an index of activity for each species at each site based on the percentage of plots on which we detected tracks during the three-night tracking session (Letnic, et al. 2009).

At each sub-site, we assessed abundances of macropods by counting the number of kangaroos (*Macropus antilopinus, Macropus agilis, Macropus rufus* and *Macropus robustus*) and northern nail-tail wallabies (*Onychogalea unguifera*) sighted while conducting spotlight surveys along single lane dirt tracks (Letnic, et al. 2009). All surveys commenced at sunset. During spotlight surveys, two observers sitting on the roof of a four-wheel-drive vehicle scanned with a 50 W spotlight, moving at a speed of 10 km/h. At each sub-site, we performed three replicate 5- 10 km spotlight surveys, each on a different track . We calculated an index of the abundance of kangaroos (*Macropus* spp.) and nail-tail wallabies, respectively, for each survey transect as the number of macropods sighted per kilometre of survey. We expressed indices of kangaroo (*Macropus* spp.) and nail-tailed wallaby abundance at each subsite as the mean numbers of animals sighted per kilometre of spotlight survey. For the purposes of structural equation modelling (see below) the indices for *Macropus* spp. and nailtail wallabies were summed together to make the variable macropod activity.

At each sub-site, we assessed rodent abundance over three consecutive nights on eight 1 ha trapping grids that were placed at least 700 m apart. To minimize effects from livestock disturbance, the grids were established more than 2.5 km from artificial watering points. This was done because livestock movements in the rangelands of northern Australia are focal around water (Hunt, et al. 2007). On each grid, we placed 20 Type LFA Sherman traps (H.B. Sherman Traps, Inc., Florida, USA), 20 m apart, in a grid formation. Traps were baited with a mixture of peanut butter, oats, honey and fish oil. Captured rodents were identified to species level and marked with an indelible marker-pen to identify recaptures. We calculated indices of rodent abundance at each sub-site as the mean number of individuals captured per trap night.

At each sub-site, ee estimated the intensity of recent activity by cattle (*Bos taurus*) on each trapping grid by scoring their dung (Hoffmann 2000, Ludwig, et al. 1999). On each grid we scored the presence of groups of recent dung (indicated by the presence of a black patina) on two 1 x 100 m belt transects on each study grid. We calculated an index of grazing intensity for each grid as the mean number of groups of fresh cattle dung.

At each sub-site, we assessed the complexity of the understorey vegetation on each trapping grid by sampling within four 5 x 5 m quadrats, placed in each corner of the grid. Within each quadrat, we recorded the percentage of a 20 - 50 cm chequered cover board obscured by vegetation within five strata (0 – 20, 20 – 50, 50 – 100, 100 – 150 and 150 – 200 cm) above ground level (Colman, et al. 2014). Because previous studies have shown that fire can simplify vegetation structure and thus influence small mammal assemblages (Legge et al. 2008), we classified each trapping grid as being burnt in the last 12 months or as not being burnt for more than 12 months based on the presence/absence of indicators of fire such as ash on the ground surface and fresh fire-scarring on trees and shrubs.

Statistical analysis: meta-analysis

As the dominant vegetation communities of the paired-sites differed and we sampled each at a different time, we treated each paired-site as an independent comparison of the effect of dingo population control and pooled the results of these comparisons using a meta-analytic approach (Colman, et al. 2014). Specifically, we used random-effects, meta-analysis to test our **a priori** hypotheses regarding the effects of dingo control on the measured response variables. This approach allowed us to determine whether the biological effects of dingo control were consistent among sites and if the mean effect of dingo removal differed significantly from zero. We used a random-effects meta-analysis because this approach assumes that estimates of treatment effect can vary across studies because of real differences in treatment effects between case studies in addition to sampling variability (Rosenberg, et al. 2000). In the case of our study, we expected the effects of dingo control to vary among the paired-sites owing to differences in the intensity of poison baiting and longevity of each baiting programme at the baited sites (Appendix S1). We used Hedge's d as the metric of effect size. We considered mean effect size statistically significant if the bias-corrected bootstrapped 95% CIs calculated from 999 simulations excluded zero (Gurevitch and Hedges 1999). We conducted analyses using METAWIN v. 2 (Rosenberg, et al. 2000).

Structural equation modelling

We used piecewise Structural Equation Modelling (SEM) (Grace, et al. 2012) to test hypotheses based on *a priori* knowledge of interactions thought to occur between the abundances/activity of dingoes, cats, macropods (*Macropus* spp. and nailtail wallaby pooled) and native rodents, vegetation cover, cattle grazing activity,the occurrence of fire and dingo baiting. We fitted all localized estimates within our SEM using Generalised Linear Mixed-Effects Models (GLMM) with a Poisson or Gaussian (vegetation model only) error distribution. We included survey area (i.e., the location of the seven paired sites) as a random factor in all analyses to account for biogeographical and temporal variation between sites. For the Poisson models, dependant varibles were treated as whole number by multiplying the proportional data by 100. Deviance explained (1 – null deviance / model deviance) and conditional R^2 values were used to assess model fit for the separate generalised and linear mixed-effects models, respectively .

We populated an initial *a priori* SEM with data from our field survey. Because dingoes, cats, and macropods are relatively large animals with large home-ranges, we sampled their abundances using the track (dingoes, cats) and spotlight (macropods) survey data at the site scale (i.e. n = 14). Because native rodents in the study area have home-ranges less than the mean distance between sample grids (mean distance 1 km) (Breed and Ford 2007), we sampled their abundances using the live-trapping sampling method at the grid scale (i.e. n = 112). Measurements of vegetation cover, mean annual rainfall and the occurrence of fire in the previous year were made at the grid scale. We used a backwards step-wise elimination process for model simplification, whereby we sequentially deleted non-significant pathways from models until only significant ($P < 0.05$) pathways remained. We calculated standardised path coefficients and deviance explained for these most parsimonious models using the protocol described in (Grace, et al. 2012). Recognising the post-hoc nature of model selection, we treated the resulting model as a hypothesis, useful to compare with our *a priori* SEM model and for further research. We performed all statistical analyses in R Version 3.0.3.

We constructed our *a priori* SEM model based on trophic cascade theory, the mesopredator release hypothesis, and prior knowledge of the factors hypothesised to influence vegetation structure and the abundances of mammals in northern Australia. Our SEM included the following hypothesised pathways (Fig 1a): 1) 1080 baiting should negatively affect dingo activity, as dingo populations decline following baiting programs (Thomson 1986); 2) dingo activity should negatively affect cat activity owing to direct killing or competitive exclusion (Brook, et al. 2012), but 1080 baiting should have no direct effect on cats because cats rarely take baits targeting dingoes (Doherty, et al. 2017, Risbey, et al. 2000); 3) dingo activity should negatively affect macropod grazing intensity by suppressing macropod abundance through direct predation (Morris and Letnic 2017); 4) cat activity should negatively affect rodent abundance owing to predation (Frank, et al. 2014, McGregor, et al. 2014). Although dingoes are predators of rodents, we did not include a pathway between dingoes and rodent abundance in our SEM. This is because consistent with the findings of a previous study (Gordon, et al. 2017) preliminary models showed a positive correlation between these variables and there was no biologically plausible *a priori* reason to hypothesize that dingoes have a direct positive effect on rodents; 5) abundance of macropods and cattle grazing activity should negatively affect ground cover from grazing (Ash, et al. 1997, Morris and Letnic 2017); 6) exposure to fire should negatively affect vegetation cover between 20 – 100cm, as ground cover is reduced immediately after fire (Legge, et al. 2008); 7) rainfall should positively affect vegetation cover between 20 – 100 cm by promoting plant growth (Ash, et al. 1997, Radford and Andersen 2012); and 8) vegetation cover should positively affect native rodent abundance, as previous studies have shown increasing rodent abundance with increasing ground cover (Fisher, et al. 2014, Kutt and Gordon 2012).

RESULTS

Paired site comparisons

The effectiveness of poison baiting at reducing dingo populations was demonstrated by the greater activity of dingoes at unbaited than baited sub-sites (Figures 2a, 3a). Conversely, and as predicted, cat activity was on average greater at baited than unbaited sub-sites (Figures 2b, 3a). As predicted, the abundances of nail-tail wallabies and kangaroos (*Macropus* spp.) weregreater at baited than unbaited sub-sites (Figs. 2c, 2d, 3a).

Rodent species captured were *Rattus tunneyei, Melomys burtoni, Pseudomys delicatula, Pseudomys nanus, Leggadina lakedownensis, Mesembriomys gouldii* and *Notomys alexis*. On average, the abundance of rodents was greater at unbaited than baited sites (Figures 2e, 3a).

Grazing activity of cattle, as estimated by counts of dung, did not differ between baited and unbaited sites (fig. 3a). On average, the density of understory vegetation between 0 – 100 cm (Figures 2f, 3a) above ground level was greater at unbaited than baited sub-sites. Density of understorey vegetation between 100 and 200 cm above ground-level did not differ between baited and unbaited sites (Figure 3a).

Structural equation modelling

The following pathways were excluded from the most parsimonious model: vegetation cover effect on rodent abundance (unstandardized coefficient estimate '*c.e.*' = -0.011, *P* = 0.671), the effect of fire on vegetation cover (*c.e.* = 2.124, *P* = 0.212), and the effect of cattle on vegetation cover (*c.e.* = -0.340, *P* = 0.159). We included all other variables/pathways within the final SEM model (Fig. 1b). Dingo baiting correlated negatively with dingo activity (Fig. 1b, 4a; *c.e.* = -0.993, *P* < 0.001). Similarly, in accordance with the *a priori* SEM model, dingo activity correlated negatively with cat activity (Fig. 1b, 4b; *c.e.* = -3.573, *P* = 0.007) and cat activity was correlated negatively with rodent abundance (Fig. 1b, 4d; *c.e.* = -17.613, *P* = 0.031). Thus, dingo baiting had a negative, indirect relationship with rodent abundance mediated through both dingoes and cats (Fig. 1b). Also in line with our *a priori* SEM model, dingo activity correlated negatively with macropod abundance (Fig. 1b, 4c; *c.e.* = -9.746, *P* < 0.001) and macropod abundance was correlated negatively with vegetation cover (Fig. 1b, 4e; *c.e.* = -2.375, *P* =0.001). Thus, dingo baiting had a positive, indirect relationship with grass cover mediated through both dingoes and macropods (Fig. 1b).

DISCUSSION

Differences in the structure of ecosystems at sites where dingo populations were controlled versus uncontrolled accorded well with our *a priori* predictions generated from trophic cascade theory and the mesopredator release hypothesis. As predicted by trophic cascade theory, macropod abundance was greater and understorey vegetation (<100 cm above ground-level) was sparser at sites where dingo populations were controlled. As predicted by the mesopredator release hypothesis cat activity was greater and native rodent abundance was lower where dingo populations were controlled. In common with studies conducted in desert (Fig 3b) and forest (Fig 3c) biomes of southern Australia, the effect of dingo control on mammal species scaled with their body size. In our study,mammals weighing less than 700 g such as rodents tended to be recorded less often in baited areas while mammals weighing more than 4000 g such as nailtail wallabies and kangaroos tended to be observed more often at sites where dingoes were controlled. Taken together, our results are consistent with the idea that removal of dingoes triggers ecological cascades along multiple interaction pathways mediated by herbivores and mesopredators, respectively.

As with most previous research on the effects of manipulating dingo abundance (Letnic, et al. 2012), our study did not involve an experimental manipulation of dingo abundance but instead utilised pre-existing land-management frameworks – the presence or absence of dingo population control – for the experimental treatment. Thus we cannot rule out the possibility that another source of environmental variation may have produced the ecological patterns we report. However, concordance between our results and our *a priori* predictions generated from theory and the extensive spatial spread of the paired baited/unbaited study sites provide considerable support for the idea that dingo control drives shifts in the composition and architecture of savannah ecosystems (Ford and Goheen 2015). Moreover, our findings that dingo control is linked to increases in the abundances of macropods and feral cats and decreases in the density of understorey vegetation and abundances of rodents are remarkably consistent with the findings of previous studies that investigated the effects of dingo control in desert and forest ecosystems (Colman, et al. 2014, Wallach, et al. 2010) (Fig. 3b,c). Therefore, we contend that it is unlikely that any other source of variation, other than the presence/ absence of dingo control, could have caused the consistent effects that we report with respect to trophic group/taxon and body size. However, because our results were based on correlations, we recommend that further studies, and in particular, manipulative experiments, are undertaken to provide more fine-scale resolution on the effects that dingo removal has on tropical savannah ecosystems.

In accord with trophic cascade theory (Schmitz, et al. 2000), our results revealed a positive association between dingo removal and macropod abundance and a negative association between dingo removal and vegetation cover below 100 cm (Fig. 2b, 4a). This pattern is consistent with the hypothesis that removing apex predators releases herbivores from direct predation pressure and that the associated increase in grazing pressure results in depleted plant biomass (Schmitz, et al. 2000). That understorey vegetation cover was also positively correlated with rainfall in the previous 6 mont suggests that understorey vegetation cover in this region is a function of both bottom-up and top-down effects. The idea that dingo control induces trophic cascades in tropical savannahs is consistent with the findings of studies conducted in arid and forest ecosystems which have linked suppression of dingo populations to irruptions of macropods and reduced understorey vegetation cover, respectively (Colman, et al. 2014, Morris and Letnic 2017).

As predicted by the mesopredator release hypothesis (Crooks and Soule 1999), feral cat activity was greater at baited than unbaited sites and was negatively correlated with dingo activity in our SEM (Fig. 1b, 3a). Other studies conducted in the northern tropics of Australia found similar results, providing evidence that cats avoid dingoes in space and time (Brook, et al. 2012, Wang and Fisher 2012), and that dingoes suppress the abundance and activity of feral cats (Brook, et al. 2012, Brook and Kutt 2011, Kennedy, et al. 2012). These effects that dingoes have on cats are thought to arise because cats are at high risk of being killed if they encounter a dingo (Moseby, et al. 2012).

Consistent with the mesopredator release hypothesis, our results showed that, on average, the abundance of native rodents was lower in areas subject to dingo control and there was a negative correlation between rodent abundance and cat activity in our SEM. However, it is important to note that rodents were captured infrequently at most of the study sites (Fig. 2e). The rarity of small mammals across the region is consistent with studies which have reported declines of small mammals in northern Australia in recent decades (Frank, et al. 2014, Woinarski, et al. 2011). Declines of small mammals in northern Australia have been attributed to multiple drivers including predation by feral cats, removal of vegetation by livestock and shifts in fire regime and the interaction between vegetation removal and predation by feral cats (Fisher, et al. 2014, Lawes, et al. 2015, Leahy, et al. 2016, Legge, et al. 2008). Our results showing a strong, non-linear negative relationship between cat activity and rodent abundance whereby the highest abundances of rodents occurred at sites where cats were not recorded and rodents occurred at low abundances at the sites with the high levels of cat activity (Fig. 4d) strengthens support for the idea that small mammal declines in northern Australia are linked to predation by cats.

A short-coming of our study is that we did not have sufficient resources available to index the abundances of medium sized marsupials (body mass 100-5000 g). Previous studies suggest that the abundances of medium-sized marsupials are likely to affected by a number of factors including predation by dingoes and cats and interactions with the impacts that fire regimes and cattle grazing have on habitat structure (Brook and Kutt 2011, Fisher, et al. 2014, Radford, et al. 2014). We recommend that further studies are conducted to investigate the effects that dingo control have on small marsupials because they are preyed upon by both dingoes and cats and thus might be expected to be affected by the relative abundances of these predators (Brook and Kutt 2011, Kutt 2012).

Our findings that dingo control is linked to increased abundance of macropods and activity of feral cats have implications for managing tropical savannah ecosystems in northern Australia. Irruptions of macropods associated with dingo suppression likely reduce the availability of pasture for livestock and removes vegetation required as habitat or shelter from predators by small mammals (Leahy, et al. 2016). Predation by feral cats has been mooted as a key driver of mammal declines in northern Australia (Fisher, et al. 2014, Lawes, et al. 2015). Hence, an increase in the abundance or activity of feral cats associated with dingo control is likely to result in higher predation pressure on small mammals. Our results suggest that maintaining dingo populations can help mitigate the negative impacts that feral cats may have on small mammals in northern Australia. A further management implication of our study relates to the fact that the number of 1080 baits deployed each year to control dingoes has steadily increased over time in the study region (Fig. S2, Supplementary Information). Thus, we speculate that the impacts of 1080 baiting on dingoes and northern Australian ecosystems has increased over time and will continue to increase if the upward trend in annual 1080 useage continues.

Our findings have significance for understanding of trophic cascades because they provide evidence that removal of an apex predator can influence the composition and architecture of ecosystems via multiple ecological pathways. While previous studieshave shown that relaxation of apex predators' effects on herbivores and mesopredators can induce trophic cascades, most have considered just one ecological pathway in isolation (Ripple, et al. 2014). We suggest that the focus of most previous studies on a single trophic pathway likely stems from logistic constraints. Indeed in some instances parallel studies provide evidence that apex predators can initiate trophic cascades along multiple trophic pathways (Beschta and Ripple 2016, Newsome and Ripple 2015). Similarly, predator removal experiments conducted on rocky shore ecosystems show that predators' effects can propagate along multiple interaction pathways (Paine 1980). Taken together, the results of this study, and earlier studies investigating the effects of dingo removal in desert and forest biomes suggest that dingoes' suppressive effects on herbivore and mesopredators occur at the same time (Colman, et al. 2014, Letnic, et al. 2009). Consequently, restructuring of ecosystems associated with removal of apex predators is likely to result from simultaneous trophic cascades triggered by apex predators' suppressive effects on both mesopredators and herbivores. Concordant effects of dingo removal across tropical savannah, forest and desert ecosystems provides support for calls that top-down forcing should be considered a fundamental process governing the function and structure of ecosystems (Estes, et al. 2011).

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FIGURE LEGENDS

Figure 1: (a) *A priori* piecewise structural equation model describing native rodent responses to dingo baiting in the northern tropics of Australia. (b) Most parsimonious structural equation model showing direct and indirect interaction pathways influencing rodent abundances. Path co-efficient estimates shown alongside arrows and deviance explained (d.e.) beside eachvariable. Dashed lines represent negative interaction pathways, and solid lines represent positive interaction pathways. Grey polygons show sections of the structural equation model sampled at the sub-site scale (n = 14), and white polygons show sections of the structural equation model sampled at the grid scale (n = 112).

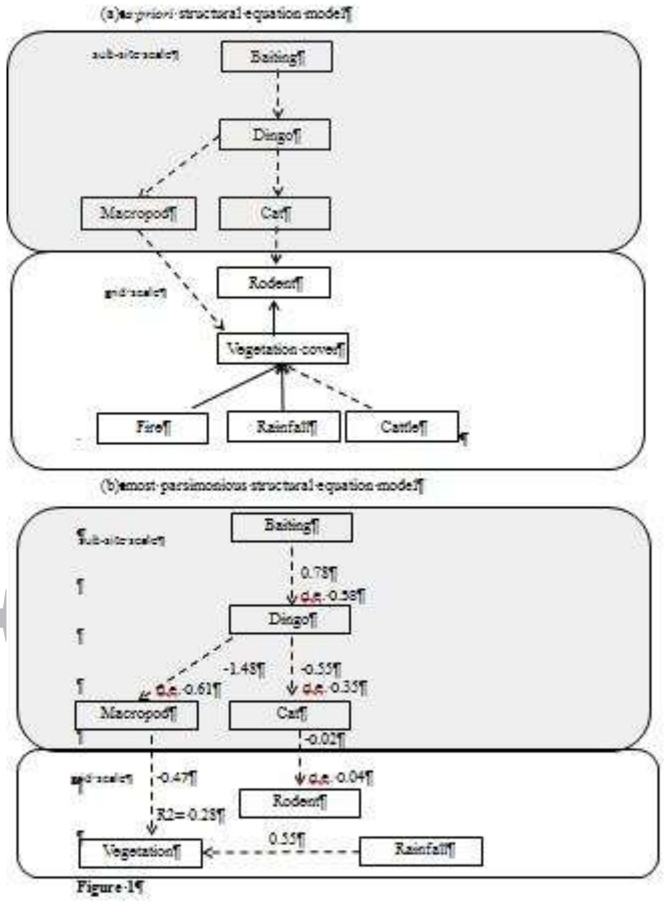

Figure 2: Mean (+ s.e) (a) dingo activity, (b) cat activity, (c) *Macropus* spp abundance (d) nailtail wallaby abundance (e) rodent abundance and (f) understorey vegetation density 0-100 cm above ground-level at the sub-sites where dingo populations were controlled using poison baits (black bars) or not controlled (grey bars) at each of seven sites in northern Australia.

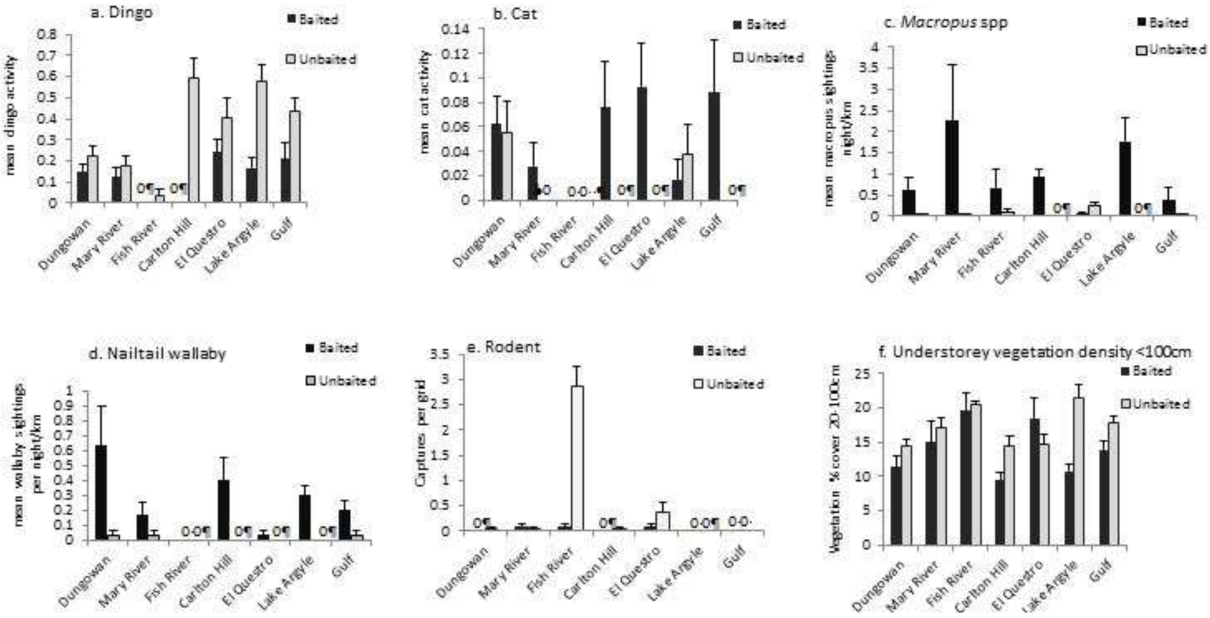

Figure 3: Mean effect size (hedges d) of dingo control ± 95% bias-corrected bootstrapped confidence intervals (Cls) for variables (a) in this study and from studies of the effects of dingo control on (b) desert ecosystems in Australia (adapted from (Letnic, et al. 2009)) and (c) forest ecosystems in Australia (adapted from (Colman, et al. 2014)). Negative values indicate variables that decreased where dingoes were poisoned and positive values indicate variables that increased where dingoes were poisoned. The mean effect size was considered statistically significant if the 95% Cls excluded zero. Values in parentheses indicate the body size range of species or height of the vegetation stratum.

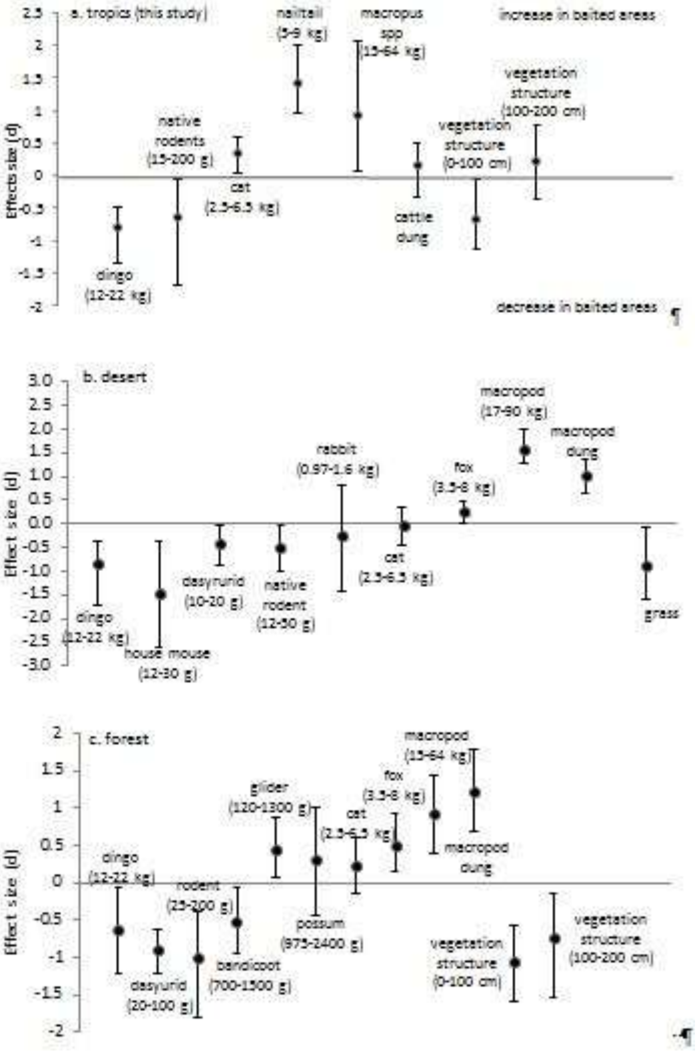

Figure 4: Raw data plots for important pathways in the most parsimonious structural equation model describing native rodent responses to dingo baiting in the northern tropics of Australia. (a) Mean dingo activity at baited and unbaited sites. (b) Relationship between cat activity and dingo activity. (c) Relationship between macropod and dingo activity. (d) Relationship between rodent activity and dingo activity. (e) Correlations between vegetation cover and macropod activity.